The background of the book cover features three fossilized hominid faces. The central face is the most prominent, showing a large, dark, textured skull with a prominent brow ridge and a slightly open mouth. To its left and right are two other faces, partially obscured and less distinct, suggesting a range of human evolution. The overall tone is dark and textured, with a mottled brown and black background.

Ian Tattersall

The Fossil Trail

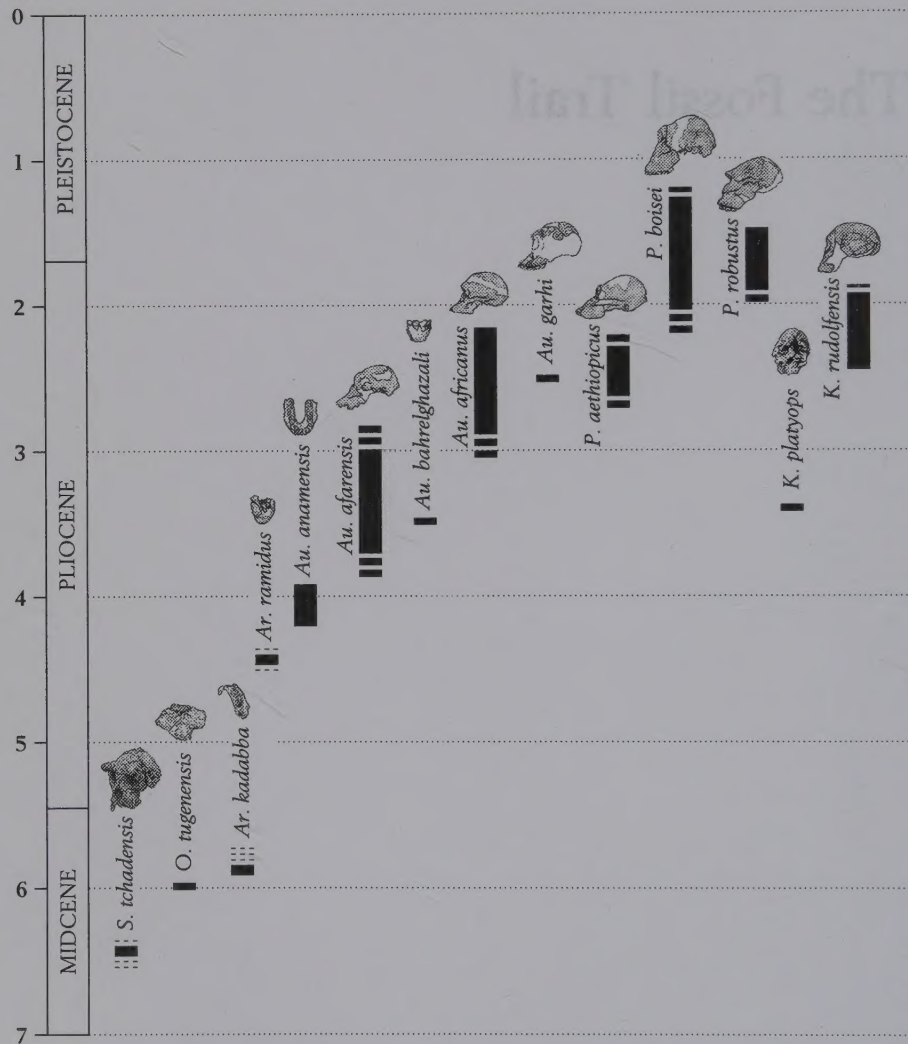
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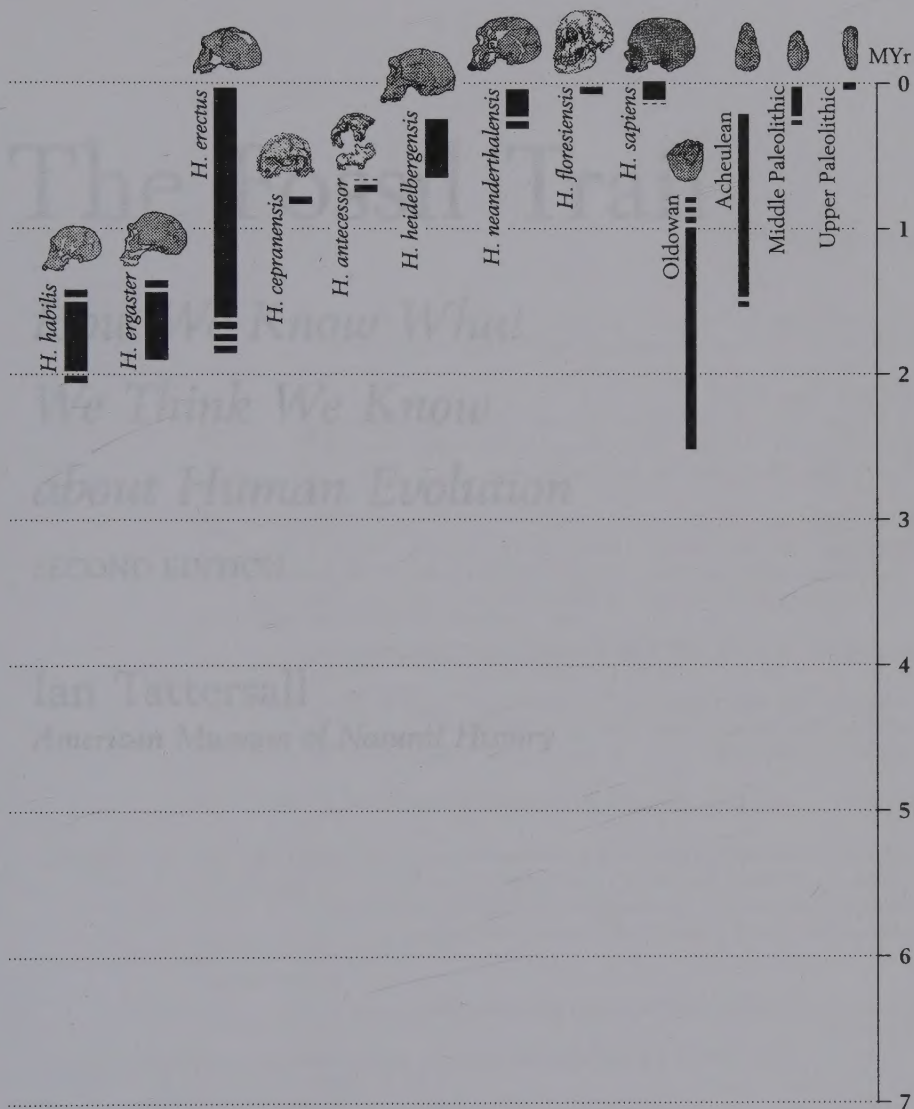
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The Fossil Trail

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*How We Know What
We Think We Know
about Human Evolution*

SECOND EDITION

Ian Tattersall

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For Jeanne

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PREFACE

In my preface to the original version of this book, completed in 1993, I wrote of the provisional nature of scientific knowledge and of how susceptible it is to modification. In the decade and a half that has elapsed since then, events in paleoanthropology have not only borne out this observation, but have also shown how resistant science can be to change. The numerous accretions to the hominid fossil record during this period have made it one of the most exciting in paleoanthropological history, with one discovery after another strengthening the unmistakable signal of diversity in the record of our biological past. Yet we still do not have a systematic scheme that is adequate to accommodate the extraordinary variety now at hand. With luck, future historians will record a paradigm shift in the first quarter of the twenty-first century that finally brought systematic concepts into line with the evidence; meanwhile, in this revised and expanded edition of *The Fossil Trail* my wish is simply to document the major new hominid fossils reported since 1993, to outline how they have been interpreted, and to provide a glimpse into the increasing role of technology in advancing our interpretation of the evidence we have.

It was difficult to know how best to revise *The Fossil Trail*. The book is an essentially chronological account of the discovery and interpretation of the hominid fossil record; yet it is more complexly structured than I had initially realized, and extensive rewriting throughout would have transformed the book in a way that I considered undesirable. Wishing to remain as true as possible to the original, I have thus only lightly revised the original chapters (with the exception of Chapter 16) and have brought the story up to date principally by adding two long new chapters at the end, ahead of a rewritten summary chapter. Although these additions change the balance of the final part of the book a little, I hope that the end result will be helpful to anyone trying to understand where paleoanthropology stands near the end of the first decade of the new millennium. The final chapters of the book are,

of course, a history of my own times, and they occasionally concern debates that I have personally been involved in. A temptation to editorialize was thus inevitable, though I hope I have contrived to keep it under reasonable control.

Acknowledgments

No book like this one could have been written without the help or influence of very many colleagues. These are too many to be named individually, although most have been identified somewhere in the text. Thank you all.

My American Museum of Natural History colleagues Niles Eldredge, Eric Delson, and Richard Milner were kind enough to read the original manuscript and to offer valuable suggestions. The same service was rendered in the case of this new edition by Will Harcourt-Smith and Rolf Quam. None of these kind colleagues will have agreed with all that is said here, but all have my gratitude. Gisselle Garcia provided essential assistance throughout and also merits my warmest thanks.

Paleoanthropology is above everything a visual science, and good illustration is of critical importance. I was fortunate indeed to work in the preparation of the original edition with Don McGranaghan and Diana Salles, who did the artwork in Chapters 1–16. The work of each is identified by initial at the end of the individual figure captions, and my deepest appreciation goes to both. The added chapters in this revised version are illustrated by photographs whose sources are acknowledged in the captions. Many thanks to all those kind colleagues who contributed them.

The original edition of *The Fossil Trail* would never have been started without the vision of Bill Curtis or finished without the persistence and patience of Kirk Jensen. The existence of this revised version reflects the confidence and encouragement of my current OUP editor, Jan Beatty. I am most grateful to all, as I am to Cory Schneider, Lauren Mine, and to Mary Aranes and her colleagues on the OUP production staff.

Finally, once again my deepest appreciation goes to the American Museum of Natural History, both for affording me the opportunity to write, and for the incomparable ambience in which I have been able to do it.

PREFACE TO THE FIRST EDITION

Sir Isaac Newton (among others) once said that if he had seen farther, it was because he had stood on the shoulders of giants. In these gracious and unusually modest words he acknowledged a debt to the past that is universal among scientists—and also, if unintentionally, a burden that is equally ubiquitous. For although every scientist starts from a base established by his (or her) predecessors, what he sees from his lofty elevation depends on how tall his giant is, and in what direction he happens to be facing. That's what this book is about, for how you read your evidence is often at least partly conditioned by what you are expecting to find; and in the science of paleoanthropology preconception may well have played a larger role than in most other sciences. Of course, the study of human evolution has come a long way since its early days, in terms both of the basic fossil evidence and of how it is analyzed. But we are still largely in thrall to received wisdom, and this brings us back to the central theme of this book. How—and why—have we come to believe what we think we know about human evolution: about the complex history of our own biological past?

Most popular books about human evolution in recent years have been based on the experience of individual paleoanthropologists in the field, and thus have at least implicitly projected the notion that reconstructing the past is essentially a matter of discovery: find enough fossils, and all will be revealed. This in turn reflects the idea that paleontology is somehow like a giant jigsaw puzzle, and that once we have all the pieces they will fit together to disclose the full picture; or at the very least, that when we have enough pieces we will be able to discern the broad outlines of the design.

Hence the traditional paleontologists' lament: the inadequacy, almost invariably described as "woeful," of the fossil record. Well, it's true that we will never have a "complete" fossil record. In fact, we will never have a human fossil record that preserves even a thousandth of one percent of all the individuals that have ever lived. But even now we have a reasonably good—and constantly improving—sampling of fossil species that should allow us, by

appropriate analysis, to gain a provisional idea of the major events that led to the emergence of our own kind on the earth. I use the term "provisional" in a positive sense, because all scientific knowledge is provisional; indeed, how can we expect to make progress in any area of science if what we believe now is not somehow inaccurate or at least incomplete? A scientific idea is one that can be tested in the light of new observations, whether these new observations are experimental, or are based on new discoveries or on new analyses of old discoveries. Popular misconceptions to the contrary, scientific ideas are not declarations of immutable truth, and are not intended to be.

But the starting point for any new set of hypotheses is the set of hypotheses that preceded it; and what we believe today can never be fully independent of what we believed yesterday. Moreover, in anything as close to our own ego as the story of our own origins, what we think we know cannot be independent of what we believe about ourselves. Clearly, it is too much to ask that scientific opinions in this emotive realm should be entirely independent of prevailing social thought and attitudes. So in trying to comprehend how we know what we think we know today about our evolution, it's important to look back at the past of paleoanthropology, and to understand by what circuitous routes we have arrived at that knowledge. What we have believed in the past, what evidence we have now, and how we look at that evidence, all interact in a complex way. Which is why this book follows a historical path.

ABBREVIATIONS

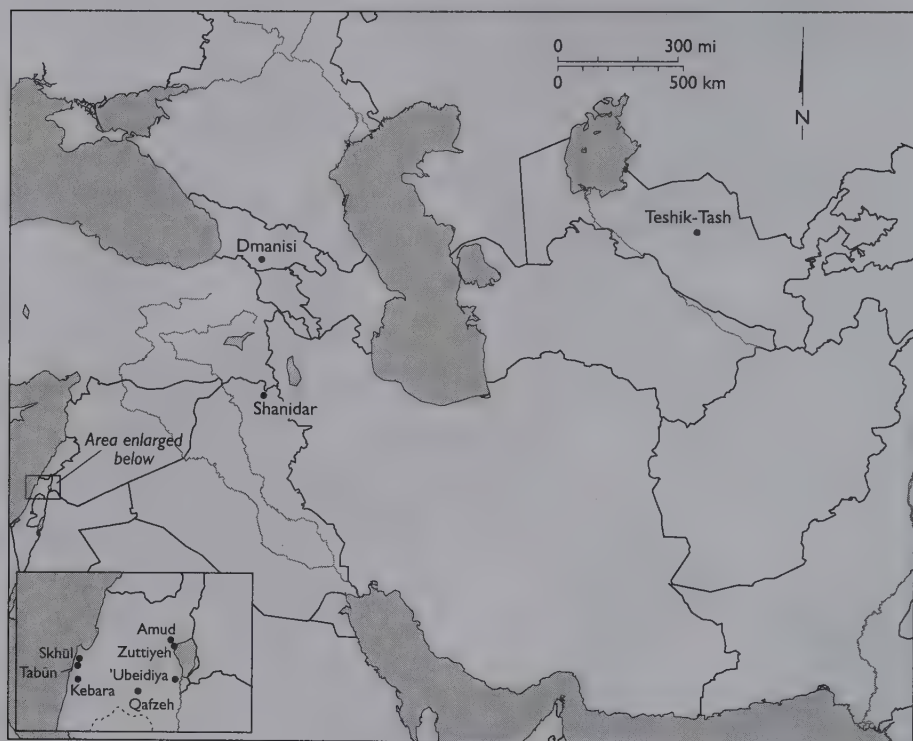
AMNH	American Museum of Natural History
DK	Douglas Korongo (a locality at Olduvai Gorge)
FLK	Frida Leakey Korongo (a locality at Olduvai Gorge)
FLKNN	FLK North (a locality at Olduvai Gorge)
KBS	Kay Behrensmeyer Site (at East Turkana)
KNM	Kenya National Museums
KNM-ER	Kenya National Museums—East Rudolf
KNM-WT	Kenya National Museums—West Turkana
LH	Laetoli Hominid
MLD	Makapansgat Limeworks Deposit
MNK	Mary Nicol Korongo (a locality at Olduvai Gorge)
NME	National Museum of Ethiopia
MNE-AL	National Museum of Ethiopia—Afar Locality
NMT	National Museum of Tanzania
NMT-WN	National Museum of Tanzania—West Natron
OH	Olduvai Hominid
SK	Swartkrans
Sts	Sterkfontein
TM	Transvaal Museum
UW	University of the Witwatersrand



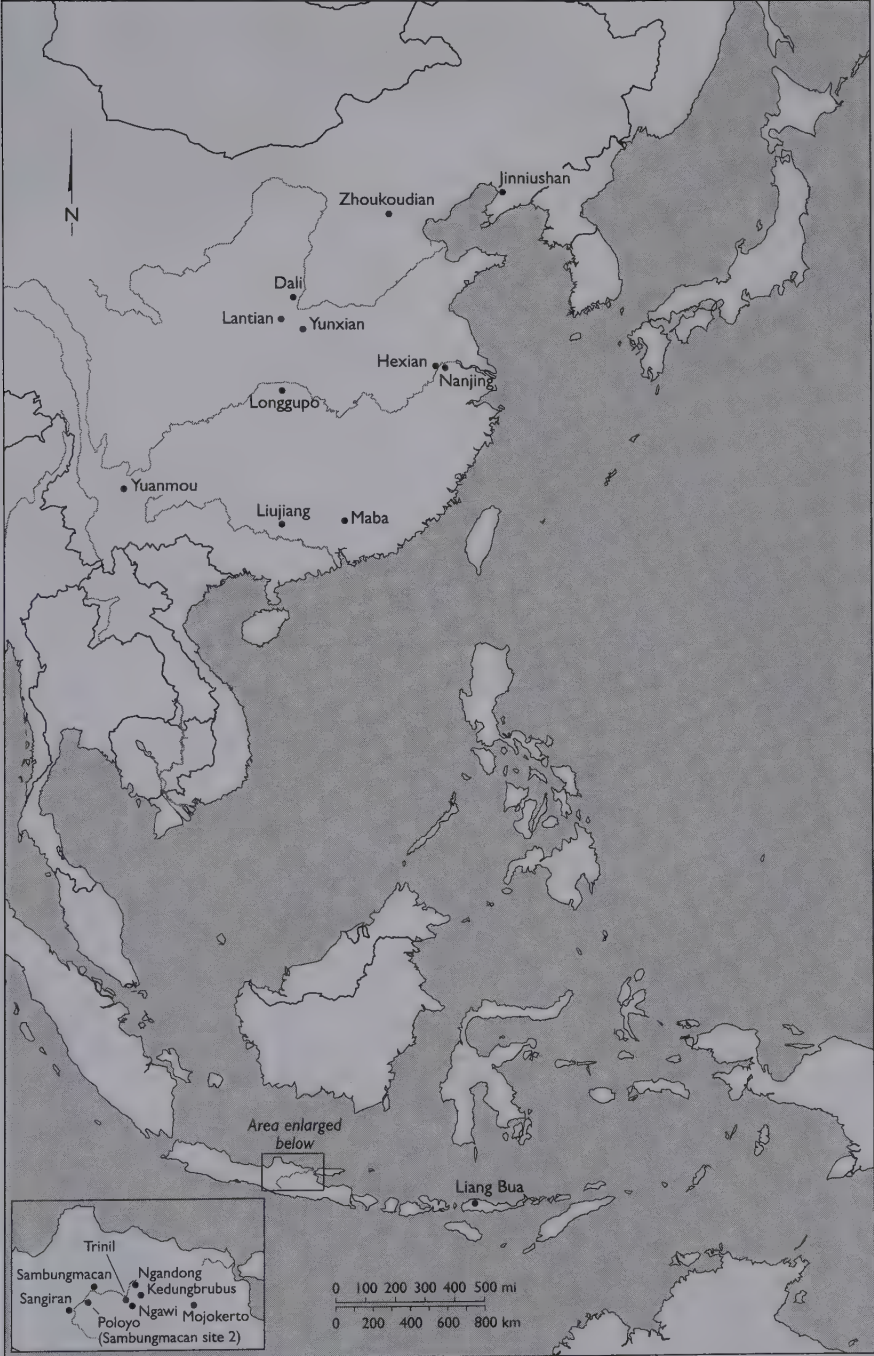
Site Map of Western Europe



Site Map of Central Europe



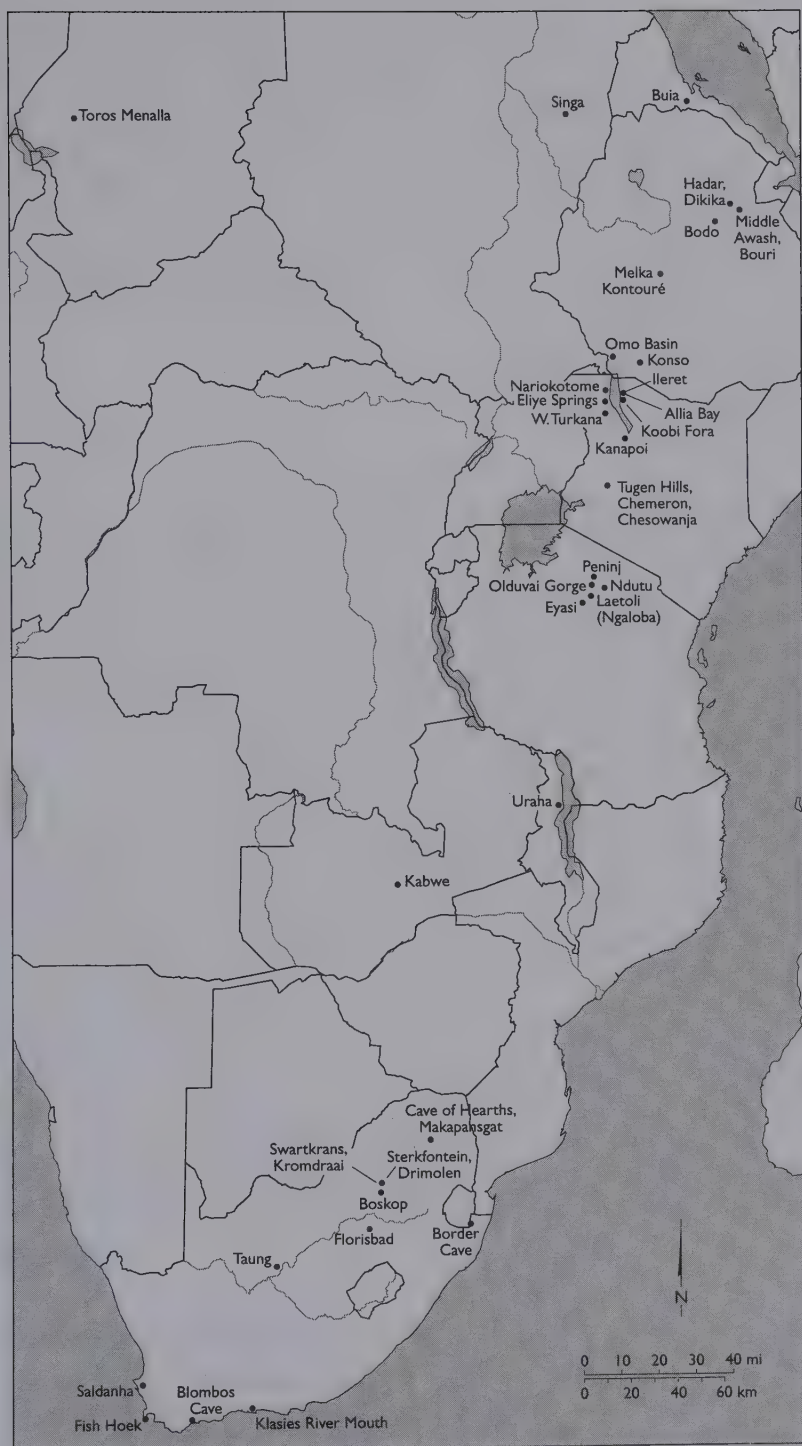
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Site Map of East Asia



Site Map of Northern Africa



Site Map of Southern Africa

CHAPTER 1

Before Darwin

Interest in our own origins dates back to a time well before anyone realized that we had a fossil record, or even an evolutionary past. Indeed, every human society has its own origin myths, reflecting the need for self-explanation that seems to be so deeply ingrained an aspect of the human psyche. Nonetheless, Western scientists first studied human fossils for much the same reason that mountaineers have always scaled peaks: simply because they were *there*. Of course, by the mid-nineteenth century, when the human fossil record began to yield up its secrets in abundance, there was already intense interest in the remarkable diversity of the living world and in humankind's place within it. This was matched by an increasing awareness that the world had to be a much older place than Scripture (at least as translated into seventeenth-century English) appeared to suggest. Actual fossil humans, though, were co-opted rather late into evolutionary and geological schemes, and many of the early explanations for the differences between ourselves and, say, the original Neanderthaler (discovered in 1856) had a somewhat *ad hoc* flavor to them. Certainly, reading these imaginative speculations today, one hardly gets the impression that they were informed by any body of theory or expectation, coherent or otherwise. An unkind observer might remark that over the past century and more, the practice of paleoanthropology—the study of human evolution, principally through the fossil record—has continued to plough a furrow rather distinct from mainstream evolutionary biology; but perhaps a certain insularity is inevitable in a study that touches ourselves as closely as this one does.

Time and the Diversity of Life

By the eighteenth century, zoologists were becoming increasingly preoccupied by the observation that had lain behind the notion of the Great Chain of Being elaborated by Aristotle in Classical times and that was subsequently co-opted into a scriptural context by medieval scholastic theologians. This observation is that an order exists in nature, such that humans resemble some

nonhuman creatures to a far greater degree than they do others. A relatively typical viewpoint of the period was that of Carolus Linnaeus (late in life ennobled as Karl von Linné), the Swedish savant who created the system of naming and classifying living things that we still use today. Linnaeus' system, much elaborated in the past couple of centuries but still intact in its essentials, consists of a hierarchy of increasingly inclusive categories. Thus Linnaeus grouped species into genera, genera into orders, and orders into kingdoms, the largest subdivision of living things.

In the order Primates, along with *Vespertilio*, the genus of the bats, *Lemur*, the genus of the Malagasy lemurs and various allied forms, and *Simia*, the genus of the monkeys, Linnaeus included the genus *Homo*. In addition to human beings, placed in the species *Homo sapiens*, this last genus contained *Homo troglodytes*, a species that embraced both of the great apes known to Linnaeus, namely the chimpanzee and the orangutan. Hardly a ripple greeted the publication of this part of Linnaeus' classification; after all, it was undeniable that of all living animals the great apes most closely resembled humans, a fact that had been elegantly demonstrated years before by the great English anatomist Edward Tyson. In comparing the anatomy of a chimpanzee with that of a human and a monkey, Tyson had shown in 1698 that the ape and the human resembled each other in forty-seven key respects, while the ape resembled the monkey in only thirty-four. No problem. As long as the idea of the fixity of species was not attacked; as long as the pattern of resemblances between species in nature was accepted as simply reflecting the will of the Creator, the simple recognition of similarities evident to the most inexperienced eye posed no threat at all to the prevailing beliefs of the day. Human beings were still distinct, separately created from the rest of nature: created, indeed, to give nature meaning. A world without people, most Europeans believed, would be a world without purpose.

Not that anyone thought the world had lacked purpose for long, even under the Biblical account of its creation. A literal interpretation of the word "day" in the translations of Genesis implied that humans had entered the world only fractionally after its creation, for a week is but an eyeblink in the approximately 6,000 years which theologians broadly agreed had elapsed since God had placed Adam on Earth. Martin Luther himself had subscribed to this figure, and numerous theologians had come up with similar ages for humankind. The date of approximately 4000 B.C. was arrived at by totting up the genealogies recounted in the Old Testament and fleshing them out with astronomical calculations of various kinds: a methodology that in some hands allowed calculations of astonishing precision. Thus John Lightfoot, Vice-Chancellor of the University of Cambridge, concluded in the mid-seventeenth century that the Creation had occurred at 9 A.M. on October 23, 4004 B.C.: conveniently at the beginning of the academic year!

But an equally beguiling aspect of theology is that, like constitutions, sacred documents usually leave ample room for interpretation according to

taste. By the waning years of the eighteenth century some naturalists were beginning to make use of loopholes in the Book of Genesis to envisage a rather longer time span than 6,000 years since the creation of the world, even though nobody as yet dared suggest that this figure was not roughly right for the origin of mankind. Especially in France, a new, theistic view became fashionable. This held that the Creator had started the ball rolling but had since more or less stuck to the sidelines, observing the unfolding of events presumably with some degree of interest but without much active involvement—at least until humans came upon the scene. The great French naturalist Georges de Buffon used this emerging interpretation to the greatest advantage. Structuring his account of Earth history along the lines of Genesis, he described seven phases of life. Humans appeared only in the sixth phase, and human modification of the natural world occurred only in the last. Thus Buffon was able to envisage a dynamic, constantly changing earth that had been in existence for tens of thousands of years. That relatively long period was essentially one of preparation for mankind, which only appeared when the world had become “worthy of its rule.”

Through the efforts of Buffon and others, by the end of the eighteenth century the idea that the Earth itself had had a long history was quite widely accepted, even though this meant that the account in Genesis had to be read as allegory. The Biblical genealogies still ruled the day, however, and the 6,000 year date for the creation of humankind continued to be accepted, by Buffon as by most others, as a decent approximation.

If the Earth had indeed had a long history, then geological observations could not be kept apart for long from discussions of that history. Before the turn of the nineteenth century another outstanding French scientist, Georges Cuvier, drew attention to the fact that the geological record is not a continuous one: that, indeed, it is marked by numerous dramatic breaks. He also noted that in any one place sediments laid down in seas might be succeeded by terrestrial deposits, only to be capped in their turn by more marine strata. Clearly, the sea had invaded the land on many occasions. Moreover, Cuvier saw that the lower down in a sequence of strata he looked, the less like the modern fauna the fossils contained in the rocks became. And he demonstrated the fact of extinction (which was resisted by many as incompatible with the perfection of Divine Creation) by his studies of huge fossil mammals that could not possibly have been overlooked by describers of the contemporary fauna if they still existed on Earth. Such fossils of ancient animals were abundant in geological deposits near Paris. These deposits consisted of superficial gravels that geologists of the time associated only with vigorous water action—though we now know that they were due to glaciation. Putting all of these observations together, Cuvier came up with the idea that the history of the world was marked by a series of “revolutions” or “catastrophes,” in which entire faunas were wiped out as land was flooded and seafloor exposed. Bowing to received wisdom, Cuvier suggested that the most recent of the extinct faunas

he had described might date back to about 6,000 years earlier, but it was not in France but in neighboring England that the the closest parallels were drawn between this most recent "catastrophe" and the Noachian flood.

Cuvier himself was always scrupulous in limiting his arguments to the evidence at hand and to avoid introducing theological considerations into them. His famous statement that "fossil man does not exist," for example, almost certainly referred simply to the fact that there were no human fossils known to him; it was later interpreters who added the implication that such *could* not exist. But even before Cuvier's major work on catastrophism appeared in 1812, the English physician James Parkinson, best known for the disease that bears his name, had seized upon his catastrophist ideas as scientific confirmation of the Biblical account of creation. The idea that the creation of human-kind represented the culmination of the divine plan, as revealed in Genesis, was further confirmed by the failure (up to that time) of paleontologists to find human bones in association with the extinct faunas, while the existence of the gravels containing extinct animals became evidence for the Deluge. But although this theme was taken up by a number of influential scholars such as the brilliant but eccentric geologist and divine William Buckland, it did not long go uncontested. The science of geology was developing apace, and Buckland's arguments were rapidly demolished by the likes of the geologist Charles Lyell, who was once described as having a mission to "free science from Moses."

Lyell it was who, in the three volumes of his *Principles of Geology*, published between 1830 and 1833, established the basic chronology of what we now know as the Tertiary Period, roughly the last 65 million years. Lyell divided this stretch of time (then, of course, unquantified in years) into, successively, the Eocene, Miocene, and Pliocene Epochs. In a later edition of his book, Lyell appended the Pleistocene Epoch to the end of the series, and other authors subsequently added the Oligocene between the Eocene and Miocene and the Paleocene at the beginning of the series. Not long after Lyell had introduced the concept of the Pleistocene, the paleontologist Hugh Falconer noted that it coincided with the Ice Ages that had been identified, first in Europe and then in America, by the Swiss geologist Louis Agassiz. The "diluvial" gravels were eventually identified as the results of one or another of the episodes of climatic cooling and consequent glaciation—expansion of montane and polar ice caps—that occurred during the Pleistocene. Much later, the concept of the "Holocene," or "Recent," was introduced to cover the last 10,000 years or so since the climate warmed up at the end of the last glacial episode. The unpredictable results of human interference with such patterns aside, however, there is in fact no reason to think that we are out of the glacial cycle that characterized the greater part of the Pleistocene.

A major upshot of the routing of Buckland by the mainstream geologists was the effective expunging of the Biblical chronology from scientific discussion after the 1830s. If the "diluvial" gravels could not be associated with

Million years ago	
0	Holocene
0.01	Pleistocene
1.8	Pliocene
5.3	Miocene
23.0	Oligocene
33.9	Eocene
55.8	Paleocene
65.5	

Sequence of geological epochs over the past sixty-five million years, as currently dated. The Paleocene through Pliocene together make up the Tertiary Period, now split into the Paleogene plus Neogene; the Pleistocene and Holocene compose the Quaternary Period. Epochs named by Charles Lyell are shown in boldface type. *DS.*

specific Biblical events, then the relevance of the Biblical timetable to the geological record vanished. Although this chronology was not forgotten by a generally devout populace, the way was open for geologists to contemplate a truly enormous antiquity for the world. As James Hutton, one of the fathers of geology, had already put it back in 1795, there was “no vestige of a beginning, no prospect of an end.”

Enter the Antiquarians

Geologists were not, of course, centrally interested in establishing the antiquity of humankind. Indeed, in the 1830s they had no evidence—or at least, only negative evidence—to bring to bear on the matter. The antiquarians, in contrast, had materials in hand that were highly germane to the issue. Imperishable as they are, stone tools form the most abundant category of evidence about the activities of early humans; but first they had to be recognized as human artifacts. Flaked flint tools had been known in Europe from time immemorial and were acknowledged to be curiosities that required explanation. Such explanations were as varied as they were imaginative: petrified thunderbolts, fairy arrows, exhalations of the clouds. In Europe, where (despite the use of gunflints) it was by then unthinkable to make cutting or scraping tools from stone when so many other superior materials were available, it did

not occur to anybody that these strange objects might have a prosaic explanation—until, that is, the New World was discovered, for there people still did make and use stone tools. At that point the ingredients, if not the intellectual environment, were available to facilitate a correct diagnosis. The first person to publish the idea that the “thunderbolts” were the artifacts of ancient “pre-Adamite” humans was Isaac de la Peyrère of Bordeaux, in 1655. Alas, poor Isaac suffered for his temerity, finding himself seized by the Inquisition and his book publicly burned on the streets of Paris.

In England a more tolerant if not more receptive social climate reigned. Shortly after de la Peyrère’s book appeared, Sir William Dugdale, author of a survey of the antiquities of Warwickshire, illustrated a stone axe which he claimed had been made by Ancient Britons who lacked the use of metals. Dugdale’s proposition was generally ignored, but several similar suggestions appeared in the years following; and during the eighteenth century, a somewhat less doctrinaire period than its predecessor, several French scholars, including the renowned botanist Antoine Laurent de Jussieu, took up the theme that stone tools were the work of people who knew nothing of metals. Sadly, however, the significance of the first discovery of extinct animals in association with human bones and stone tools, in the Gaylenreuth Cave in Germany, was denied even by its discoverer. In 1774 Johann Friedrich Esper wrote that he “dared not presume” that the human remains at the site were contemporaneous with the animal fossils among which they were found. It was thus not until the end of the eighteenth century that John Frere, an English country squire, more or less correctly diagnosed a group of Stone Age handaxes found twelve feet down, and once more in association with the bones of extinct animals, in a gravel pit at Hoxne, in Suffolk. These, he wrote in 1800, were weapons made by people who knew nothing of metalworking; and their geological context “may tempt us to refer them to a very remote period indeed, even beyond that of the present world,” by which he meant, of course, the 6,000-year world of Biblical chronology.

Prescient as they were, Frere’s remarks went as unheeded as their predecessors. So did the first discovery of stone tools and the bones of extinct animals in association with an extinct kind of human. This occurred about 30 years later at the cave of Engis, in a valley wall of the River Meuse, near Liège in Belgium. The excavator of the site, Philippe-Charles Schmerling, recognized the artifacts as the work of ancient people; but when he found himself unable to pay his printer, most of the copies of his great work on the *Bones of the Caves of the Province of Liège* were sold for scrap paper, severely limiting its availability to scholars. Moreover, of the two human skulls that Schmerling found, one, though of quite early date, had belonged to an individual of modern form; the older one, though the remains of an extinct kind of human, looked deceptively modern because it had belonged to a child. Finally, Schmerling’s premature death and the transfer of his Engis collections to the custody of the University of Liège, which stored them in the back of a barn, almost guaranteed obscurity



Chert Acheulean handaxe (AMNH 6.9) from the Somme River Valley, France, similar to those described by Jacques Boucher de Perthes. Scale is 1 cm. DS.

for his discoveries. It is, indeed, remarkable that they survived to attract the attention they belatedly received. Although the great age of the human remains was never seriously contested—and was eventually confirmed by no less an authority than Sir Charles Lyell, who accepted their association with extinct species such as mammoths and woolly rhinoceroses—it was nonetheless many years before their true significance was recognized. A similar fate awaited an adult and much more complete archaic skull found in Gibraltar during work on military fortifications in 1848 or earlier; this also sat neglected on a shelf for many years before its importance became understood.

It is thus Jacques Boucher de Perthes, a customs official from Abbeville in northern France, who is usually credited with putting Stone Age prehistory on a firm footing. In the late 1830s, after unsuccessfully striving for acclaim as a poet and playwright, Boucher de Perthes turned his interest towards the stone tools that were being found in various places in the Somme river valley, some of them in association with extinct faunas. At first he believed that these objects were diluvian, but he rapidly abandoned Noachian explanations and came to refer to them in his voluminous works as antediluvian—from before the Flood. At that time most geologists in France were still catastrophists, and Boucher de Perthes ran into a general climate of incredulity, which was fueled by his tendency to be more than a little indiscriminating about what was and was not a tool or a fossil. He held his ground tenaciously and almost

from the beginning found some support among French scientists for his view that these objects were both tools and, as testified by the associated fossils, truly ancient.

General acceptance was long in coming, however; and the turning point only came in after the antiquarian William Pengelly and the paleoantologist Hugh Falconer, on behalf of a large committee formed by the Geological Society of London, began investigations at the Devonshire site of Brixham Cave in 1858/9. Their excavations turned up flint artifacts together with the bones of extinct mammals, and immediately a debate sprang up about the validity of the association. En route to Sicily on a geological trip Falconer visited Boucher de Perthes, hoping to find support in his collections for the relationship between the Brixham tools and bones. He found himself rapidly convinced by the Frenchman's claims, and he arranged for two eminent British scholars, Joseph Prestwich and John Evans, to visit the Somme valley in 1859. On his return to London, Evans reported to the Royal Society that the Abbevillian tools were authentic, thereby placing a quasi-official imprimatur upon the ancientness of humankind. Fittingly, that year was also the year in which Charles Darwin published *On the Origin of Species by Natural Selection*.

Paleontology

As the antiquarians were gradually demonstrating the length of humanity's history, the science of paleontology—the study of ancient life through the fossil record—was also becoming established, not least through the efforts of Georges Cuvier. But proving the existence of extinct species was one thing; admitting the transformation of one species into another was something else entirely. Cuvier, like virtually all others of his day, perceived species as static, unchanging entities, and nothing that he saw in the fossil record appeared to him to violate this conventional point of view. Faunas certainly succeeded each other in that record, but this was due to either the immigration from elsewhere of animals that had escaped destruction in the previous catastrophic episode, or the re-creations following each catastrophe. In the latter case Cuvier declined to be too specific, for, excellent scientist that he was, he did not like to mix religion and science. He was apparently not, however, prepared to contemplate the idea that one fauna—or species—could change into another.

Cuvier's beliefs were enormously influential. Elaborated by a legion of followers, they continued to dominate French geology and paleontology for decades after his death in 1832. Nonetheless, Cuvier's approximate contemporary Jean de Monet, Chevalier de Lamarck, came to believe otherwise. Cleaving for most of his career to the standard view of the fixity of species, Lamarck underwent a sort of Damascene conversion between 1799 and 1800 that radically changed his viewpoint. This change was apparently due

to his study of a collection of mollusks, in which he found that many fossil species appeared to have counterparts in the living fauna—hardly what one would expect under Cuvier's catastrophism. Moreover, Lamarck found that in many cases he could arrange his mollusks into gradually modifying series that seemed gradually to proceed from older fossil species to younger extinct species to living ones.

Deducing that such series represented connected lineages composed of ancestors and descendants, Lamarck concluded in turn that species could indeed change, slowly, from one into another. More generally, he came to the belief that the enormous diversity of species in the living world was due to the gradual divergence of lineages over vast spans of time. Such lineages, he thought, kept changing to keep pace with changing environments, and he had no problem with time: unfettered by Biblical considerations, he was prepared to contemplate a limitless Earth history. Moreover, Lamarck was even prepared to speculate that humans had arisen through this process from an apelike animal which adopted upright locomotion. These conclusions were comprehensively presented to the world in 1809, when he published his *Philosophie Zoologique*.

Having glimpsed the essential outline of the history of life, and having replaced a static concept of the living world with a dynamic one, Lamarck faced this question: If lineages change, how do they do it? Unfortunately, his choice of answer was to destroy his reputation among future historians of science. First, he proposed a sort of inbuilt tendency for organisms to become more complex, although he recognized that the actual history of life as seen in the fossil record was untidier than this would imply. An additional ingredient was needed. Since species had to be in harmony with the environment, yet environments fluctuated, species had to have a way of changing as environments changed. Lamarck thus proposed that new behaviors elicited by changing environments caused changes in the organisms themselves. The new characteristics acquired as a result of these changed behaviors would then be passed along to offspring, and gradual physical modification of the species would ensue. The starting point of this process was achieved by a sort of spontaneous generation—never precisely defined—of the ancestral species.

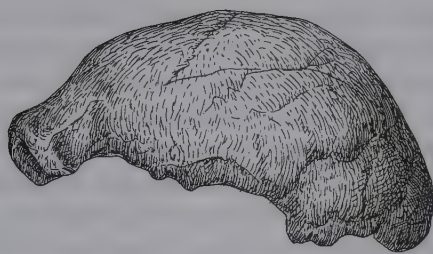
In contrast to his ground-breaking observations of change within lineages and the mutability of species, the twin notions of the modification of organs by use or disuse and of the inheritance of acquired characteristics were not new with Lamarck. But it is with these notions, and particularly with the latter, that Lamarck's name has in hindsight become associated—and by extension, the entire body of his work has appeared discredited. In his own day, Lamarck's ideas were widely and savagely attacked by scientists as diverse and influential as Cuvier in France and Lyell in England; and with the rediscovery of the principles of genetics at the beginning of the twentieth century, his

borrowed wrong ideas on the mechanism of change caused him to be reviled all over again. The result is that the baby vanished with the bathwater; but had it been Lamarck's voice, rather than Cuvier's, that had been more widely heard at the beginning of the nineteenth century, the course of evolutionary thought might have been very different.

As it was, Lamarck's insights were ignored where they were not opposed, and even among the uniformitarian geologists such as Lyell—who were, after all, busy proving that the world had in the past been shaped by the same forces that we see operating today—it continued to be believed that Earth and its contents were ultimately the handiwork of a deft Creator. It caused more than a stir, therefore, when in 1844 the London encyclopedist Robert Chambers published—anonously—a work called *Vestiges of the Natural History of Creation*. Little wonder that Chambers preferred to remain anonymous: although he accepted that a divine Creator stood behind the history of life on earth, he proposed that life has evolved through time, as the result of gradual changes that had nothing to do with catastrophes of any kind, and according to a “Principle of Progressive Development.”

Many of the points Chambers made anticipated those that Darwin was to make fifteen years later; but, albeit understandably in a nonscientist, in assembling his evidence he failed to discriminate consistently between folklore and scientific fact. What's more, he failed to come up with a convincing “engine” for evolution. Nonetheless, his book was a remarkable piece of work, even though it provoked more outrage than it did reexamination of comfortable British prejudices. And it kept alive in the minds of biologists the threat of Lamarckism, of the possibility that life had indeed changed through time. Nobody who studied living things in the mid-nineteenth century could totally ignore the possibility that something akin to evolution underlay the diversity of the living world, even if in the best of faith they denied it.

In Germany, meanwhile, the first half of the nineteenth century had witnessed the growth of *Naturphilosophie*, a romantic and occasionally rather wild-eyed movement whose adherents were reluctant to accept purely mechanistic explanations for natural phenomena—though not all of them took refuge in theological explanations of cause. Many espoused the notion of some inner impetus toward “development” in organisms, either through the expression of some preexisting potentiality or through some form of transmutation. By 1851 Chambers's book had been translated into German and had influenced such influential thinkers as Schopenhauer. German science during the 1850s was thus in a sense primed to be receptive to Darwinian ideas when they were finally published. Indeed, Hermann Schaaffhausen, the principal describer of the Neanderthal fossils, wrote in 1853, before these fossils had been found and before Darwin's book had appeared, that “the immutability of species...is not proved.” The title of Schaaffhausen's article, “On the Constancy and Transformation of Species,” reflected an active debate of the time in German scientific circles.



Side view of the original Neanderthal (Feldhofer) skullcap found near Düsseldorf, Germany, in 1856. Holotype of *Homo neanderthalensis*. Scale is 1 cm. DS.

Neanderthal Debut

It was this intellectual milieu that greeted the finding of the first human fossils recognized as sufficiently remarkable to justify a special effort at explanation. In 1856, workers began clearing out the small Feldhofer cave in the steep side of the Neander Valley (*Neanderthal*), through which the river Düsseldorf reaches the Rhine. Inside, they uncovered a skeleton buried below some five feet of mud. A few bones survived of what may, when found, have been an intact skeleton. These quickly came to the attention of a local teacher named Johann Fuhlrott. Correctly recognizing the bones as both ancient and human, Fuhlrott passed them along to Schaaffhausen, a professor of anatomy in Bonn, for fuller description. The surviving bones consisted of a skullcap, both femora (thighbones), elements of the upper and lower left arm, part of the pelvis, and a few other bits and pieces.

In many ways it is hard not to be impressed by Schaaffhausen's report, published in 1858 and translated into English by the anatomist George Busk in 1861. Schaaffhausen gave a minutely detailed anatomical description, in the course of which he remarked on the thickness of the bones and on the large size of the scars left by the muscles that attached to them. These suggested to him that the Neanderthal individual had been extremely strong and muscular, possibly as a result of a very strenuous lifestyle. Most of all, however, Schaaffhausen's attention was drawn to the unusual shape of the skullcap, and particularly to the presence of the pronounced ridges above the eyes, the large frontal sinuses, and the low, narrow forehead, which together gave "the skull somewhat the aspect of that of the large apes." These features, which he concluded were the results neither of artificial deformation nor of pathological deformity, placed the specimen beyond anything with which he was directly familiar. But what did they mean?

"Sufficient grounds exist," Schaaffhausen wrote (as translated by Busk), "for the assumption that man coexisted with the animals found in the *diluvium*; and many a barbarous race may, before all historical time, have disappeared,

together with animals of the ancient world, whilst the races whose organization is improved have continued the genus." It thus made eminent sense to search for something comparable to his specimen among the numerous existing reports of human skulls found in archaeologically ancient contexts. This Schaaffhausen did at length, even mentioning that the skull from Engis was reported to have a similarly narrow frontal bone—though he was referring to the modern-looking adult skull that Schmerling had found there, and, in any event, the truly archaic child's skull from Engis was too young to show the brow ridges that it would have acquired had the individual survived to adulthood. Although he was thus unable to identify anything in the literature that quite matched his Neanderthaler, Schaaffhausen found as a result of his survey "that a marked prominence of the supraorbital region, traces of which can be perceived even at the present time, occurs most frequently in the crania of barbarous, and especially of northern races, to some of which a high antiquity must be assigned. [So] it may fairly be supposed that a conformation of this kind represents the faint vestiges of a primitive type, which is manifested in the most remarkable manner in the Neanderthal cranium." Schaaffhausen then went on to document the savagery of various ancient European tribes (mostly as seen through the eyes of Classical or early Christian chroniclers) and to conclude that, along with various others, his specimen "may probably be assigned to a barbarous, aboriginal people, which inhabited the north of Europe before the *Germani*." Nonetheless, it is clear that Schaaffhausen was not entirely happy with this conclusion, for "the human bones from the Neanderthal exceed all the rest in those peculiarities of conformation which lead to the conclusion of their belonging to a barbarous and savage race."

Schaaffhausen's analysis is a classic example of a careful, insightful, and scholarly analysis confined by the limitations of received wisdom. By 1858 the fact that recognizable humans had first appeared in the remote past was beyond doubt; and the progressionist views prevailing in Germany made it easy to envisage that, physically or physiognomically, ancient savage tribes might have differed somewhat from civilized humans; indeed, Schaaffhausen claimed that "even in ancient times the various Germanic stocks...in proportion as they led a savage or more civilized mode of life, differed in corporeal constitution, as well as in the formation of the face and head." But as long as the idea of the mutability of species (as opposed to varieties of species) was entertained only as an abstraction, as a philosophical concept rather than as an organizing principle of the diversity of life, what Schaaffhausen and everyone else necessarily lacked was the practical idea of common descent among species (although he could think in analogous terms about "tribes"). That the Neanderthaler, so evidently human but equally evidently unlike any other human known, might represent not a variety but a relative—perhaps even an ancestor—of modern humankind was totally foreign to the prevailing mindset. It was simply too great a leap to make on the basis of a single incomplete

and rather odd-looking skull. Given that Schaaffhausen somehow had to fit the Neanderthal remains within a view of nature that, with the advantage of hindsight, we know was not appropriate, it is remarkable that he was able to achieve as balanced an analysis as he did.

In commenting on Schaaffhausen's review of this unprecedented material, Busk himself stressed the comparison between the Neanderthaler and the great apes. He also drew attention once again to comparisons with the adult Engis skull—ironically, the modern one and not the infant cranium, which, as we know now, is indeed that of another Neanderthal. But Schaaffhausen's colleague at the University of Bonn, August Franz Mayer, took issue with him on every point. Writing in 1864, five years after Darwin's publication of *On the Origin of Species*, Mayer pointed out that this skull lacked a sagittal crest—the bony ridge atop the braincase to which massive jaw muscles attach in large apes such as male gorillas. We know now that a sagittal crest is merely a passive result of combining big chewing muscles with a small braincase, and the Neanderthal braincase was a large one, containing a brain as big as our own. At the time, however, this was less apparent. "Show me a fossil human skull with a sagittal crest," Mayer demanded, "and I will admit that man descends from an apelike ancestor."

Thus refuting Schaaffhausen's interpretation, Mayer proposed two alternatives. The first was that the Neanderthal remains were those of a modern individual with pathological degeneration of the skeleton caused by childhood rickets. The shape of the femora suggested to him that the Neanderthaler was bow-legged, as many horsemen become, and he finally concluded that these were the remains of a deserter from the Cossack army that had paused in the area of the Neander Valley before crossing the Rhine in January 1814 on its way to invade France. There were also signs of trauma, duly noted by Schaaffhausen, in the surviving elbow joint of the skeleton. The individual must thus have suffered constant pain; and this, Mayer claimed, had combined with the sequelae of the rickets to cause a permanent frown. The strained facial muscles in turn had affected the shape of the eyebrow region. This reasoning sounds very quaint and amusing today, but at the time it was a theme taken up by many. Over the longer haul, though, it was Mayer's alternative suggestion to explain the peculiarities of the specimen that received most support—that the Neanderthal skull had belonged to a modern individual showing pathological changes.

What I find particularly curious about this episode is that in his 1858 paper Schaaffhausen acknowledged that Professor Mayer had early on drawn attention to dendritic encrustations on the fossil—and it was precisely on the basis of these that Fuhlrott had initially concluded that the specimens were indeed fossilized. Mayer may already have been hesitant about Fuhlrott's and Schaaffhausen's interpretations of the bones, but it nonetheless seems likely that Mayer's preferred interpretation—which, as Thomas Henry Huxley

pointed out, had a dying Cossack climbing up sixty feet of near-vertical cliff to bury himself, naked, under five feet of mud—may have had at least as much to do with the politics and personalities of the Bonn anatomy faculty as with the attributes of the specimen itself. If so, *plus ça change, plus c'est la même chose*.

CHAPTER 2

Darwin and After

As we've seen, Charles Darwin's *On the Origin of Species* did not burst forth into a world that was totally unprepared for the concept of evolutionary change—a world unwilling to accept it, perhaps, but hardly a world that was unfamiliar with most of the evidence that Darwin used to support his ideas. Certainly by 1859, the year of the great book's publication, there was more than enough evidence around to convince any open-minded observer of the reality of evolution. Darwin had been harboring his radical thoughts for nigh on thirty years, and indeed, the naturalist Alfred Russel Wallace had already come to a conclusion strikingly similar to his own in a succinct and altogether brilliant manuscript he sent back to England in 1858 from the remote Indonesian island of Ternate. Together with extracts from Darwin's writings, Wallace's manuscript, written in haste after the ideas it expressed had crystallized for its author during a bout of malarial fever, was promptly read at the Linnean Society, and it goaded Darwin into writing his book.

Remarkable though it may seem in retrospect, however, at the time few might have disagreed with the Society's president, who remarked, in his annual summing up of events, that "[t]he year has not been marked by any of those striking discoveries which...revolutionise...the department of science on which they bear." The idea of evolution was in the air in 1859, but it was not yet an idea whose time had irresistibly come. What in the end rapidly won the day for *On the Origin of Species* was not merely that Darwin was a respected naturalist to whom his peers would listen, but that in his book he documented his ideas in such eloquent, exquisite, and exhaustive detail. He produced a work of astonishing originality that, quite simply, could not be ignored, and he proposed a compelling mechanism to underpin his notions of change. It is certainly true that from the vantage point of the early twenty-first century we may tend to overestimate the influence of Darwin's ideas of natural selection on late nineteenth- and early twentieth-century evolutionary thought, but there is no doubt that, despite the resistance he initially encountered, it was Darwin who made the concept of evolution itself respectable and who set the framework for our modern understanding of how life on earth came to be the way it is.

Darwin has been the subject of numerous careers in the history of science and wrote so voluminously that by judicious quotation one can defend almost any evolutionary viewpoint as somehow "Darwinian." Nonetheless, the essentials of Darwin's theory of evolution can be quite simply expressed. His own capsule definition of evolution was "descent with modification": ancestral species give rise to descendants which do not exactly resemble them. In searching for a mechanism to explain how this might occur, Darwin faced a politico-religious problem as well as a scientific one: he had not only to come up with a plausible means of change, but also to first destroy the pervasive notion of the fixity of species. Darwin's solution was simple. His studies of barnacles had already suggested to him that species were difficult or even impossible to recognize in the living fauna, with blurred boundaries between close relatives, but he delivered the *coup de grâce* to their fixity by denying them identity in time. Here's how.

Natural Selection

In every generation, as animal breeders had long been aware, individuals of the same species vary in numerous ways. Those differences assure that some of those individuals are better suited than others to survive in any given environment. At the same time, in any generation many more individuals are born than will ever survive to grow up and reproduce themselves. It is the better adapted who will succeed in this winnowing process, and since traits are inherited, they will pass their superior adaptations on to their offspring. Each generation will thus be slightly different from the last, with more individuals possessing favorable adaptations and fewer having less well-adapted anatomies. In this way, over long spans of time, lineages will gradually become modified as they adapt to changing environments (or as they perfect their adaptations to existing environments) by the process Darwin named "natural selection."

This mechanism of change is not, Darwin stressed, in the least purposive; it consists merely of a sort of winnowing action achieved through the vagaries of the environment. Less well-adapted individuals contribute fewer offspring (resembling themselves) to the next generation, either through early mortality or through reduced reproductive effectiveness; those more favorably endowed live and produce more offspring (again resembling themselves). Most simply stated, then, natural selection is differential reproductive success.

It is central to this idea that offspring inherit their particular traits, advantageous or disadvantageous, from their parents: a fact that was obvious to anyone who had ever noted familial resemblance among relatives. Interestingly, however, Darwin had no idea how this occurred. Indeed, Darwin's theories of inheritance were totally wrong, though he has escaped the pillorying for this deficiency suffered by the unfortunate Lamarck. What is significant, though, is that Darwin was perfectly able to formulate his enduring ideas on evolution

in the absence of a valid theory of inheritance. This is a theme that we will return to later.

Now, while in one respect Darwin's ideas on evolution by natural selection ran counter to prevailing views of the fixity of species, in another way they were highly congenial to the spirit of the times in which he lived. For the Victorian ethos was one of progress, of improvement. Leave aside that the working classes labored in conditions of appalling privation; to those with the leisure to think about such matters the ubiquity of progress was evident. The explosion of technological change and economic expansion unleashed by the Industrial Revolution reached into all areas of nineteenth-century experience to inculcate a brash and optimistic view of the inevitability of progressive change and improvement. And this change was, of course, of an incremental, gradual sort: revolution was not simply undesirable, it was unthinkable. In this sense, Darwin's ideas were very much in tune with his times: whether consciously or not, he adapted to biology a more generally held notion of the inevitability of progress.

Nonetheless, once the furor that greeted the publication of his book had died down, it was for his gradualistic views on natural selection that Darwin was most strenuously criticized. Indeed, they continue to this day to be the focus of highly critical attention. In contrast, Darwin's central thesis, still the linchpin of modern evolutionary theory, was quite rapidly accepted by his peers—though it was immediately more shocking to the general public. This central thesis is that all forms of life are related by ancestry. Darwin perceived the same pattern in nature that Aristotle and others had noticed in classical times and that had been rediscovered in the seventeenth century by Linnaeus and the other early systematists as they established the science of classifying the living world. A sort of hierarchy of similarity exists in nature, such that some organisms show more mutual similarity than others. All backboneed animals resemble each other more than they resemble any animals without backbones, but within this group all mammals are more similar to each other than any is, say, to a turtle or to a hagfish. And primates have more in common with each other than any primate has with a cow or an opossum. Darwin's most basic insight was to see that this self-evident hierarchy of resemblance among living things exists as a result of genealogical relationship. This is a magnificently simple explanation for the pattern of nature, and the only one that predicts the pattern we actually find. Descent with modification: to Darwin this meant that all species, living and extinct, were descended from a single ancient ancestor, in a branching pattern that may be represented as we represent human genealogies, in the form of a tree or a branching bush.

In *On the Origin of Species* Darwin, as befitted the most cautious and unfrontational of men, was as circumspect as he could possibly have been about the implications of all this for the relationships by descent of humans—even though these implications were dazzlingly obvious. "Light will be thrown on the origin of man and his history" was all he would say at this point. But

heat, as might have been expected, ruled the day as the obvious conclusion was drawn. The most celebrated of the acrimonious exchanges that took place in the months following the publication of *Origin* was, of course, the encounter between Bishop Wilberforce and Thomas Henry Huxley, "Darwin's bulldog," at the meeting of the British Association for the Advancement of Science in June 1860, where the issues of human relatedness to the great apes were brought out into the open. At the time, the evolutionary view was widely caricatured as claiming human descent from the great apes themselves. This of course made marvellous newspaper and magazine copy; but most emphatically, the idea of common descent implies nothing of the kind. The apes, too, have become modified over the millions of years, separating us from our common ancestor, which was neither a modern human nor a modern ape.

Early Disquisitions on Neanderthals

Huxley eloquently took the bull by the horns in 1863, when he published a small book of essays entitled *Evidences as to Man's Place in Nature*. The thrust of this work was to demonstrate through comparative anatomy that the apes resembled humans much more than monkeys did. In one essay he described what was known of the history and the habits of the apes; in another he showed how embryology and anatomy demonstrate the affinities of humans to primates in general, and to apes in particular (Darwin's notion of common descent providing the only plausible mechanism for this); in the third he looked at fossils that might bear on human evolutionary history. These were limited to the adult Engis cranium, which he correctly identified as a "fair average human skull, which might have belonged to a philosopher, or might have contained the thoughtless brains of a savage," and the Feldhofer Neanderthal. He was impressed by the distinctiveness of the Neanderthal skullcap but concluded, largely because it had contained a modern-sized brain, that this specimen could not "be regarded as the remains of a human being intermediate between Men and Apes." Although "the most pithecoïd of known human skulls," it formed "the extreme term of a series leading gradually from it to the highest and best developed of human crania." It is perhaps curious that while Huxley was by instinct a saltationist who had chided Darwin in a letter that "[y]ou have loaded yourself with an unnecessary difficulty in adopting *Natura non facit saltum*—Nature does not make leaps so unreservedly," in his essay on the Neanderthaler he capitulated in just this way to the gradualist mindset.

This stance strictly limited Huxley's interpretive options. For despite the advantage of an evolutionary perspective, from which he was at least able to ask: "In still older strata do the fossilised bones of an Ape more anthropoid, or a Man more pithecoïd, than any yet known await the researches of some unborn palaeontologist?" Huxley was able to see in these specimens no more than evidence for great human antiquity. He therefore added nothing



Side and front views of the Neanderthal skull from Forbes' Quarry, Gibraltar. Scales are 1 cm. DM.

to what Schaaffhausen had already proposed—beyond, perhaps, establishing brain size as a vital criterion for humanity. Worse, in refusing to acknowledge the distinctness of the Neanderthaler, he established the basis for a unilinear view of human evolution whose leaden hand has suffocated paleoanthropology ever since.

It is hard to fault Huxley too greatly for his failure to recognize in the Neanderthaler a distinctive entity: a product, perhaps, of one of Nature's leaps. After all, the entire suite of distinctive material at his disposal consisted of one bizarre and highly incomplete specimen that was comparable to nothing else known to science. Nevertheless, a year after Huxley published his observations, the Anglo-Irish anatomist William King drew emphatic attention to the "remarkable absence" in the Neanderthal cranium "of those contours and proportions which prevail in the forehead of our species; and few can refuse to admit that the deficiency more closely approximates the Neanderthal fossil to the anthropoid apes than to *Homo sapiens*." Indeed, King argued that the specimen was so apelike as to "lead one to doubt the propriety of *generically* placing it with Man," although "in the absence of the facial and basal bones" to advocate this view "would be clearly overstepping the limits of inductive reasoning." Nonetheless, in contemplating the Neanderthal skull, King found himself compelled to conclude that the "thoughts and desires that once dwelt within it never soared beyond those of the brute," and in a footnote, suppressing his desire to place it in a separate genus, he created for the specimen the new species *Homo neanderthalensis*. King's was the first formal recognition ever that another human species besides *Homo sapiens* had existed on the Earth. And while its author was certainly bold in unhesitatingly arriving at this conclusion with just one fossil at hand, unbeknownst to him another specimen had already been found which demonstrated that the Neanderthal specimen was no aberration.

A fossil skull found in a quarry at Gibraltar had been found at some time prior to 1848, when it was brought to the attention of the Gibraltar Scientific Society. Unappreciated for what it was, it lay gathering dust in a small local museum until it was spotted by a visiting anthropologist in 1863. This gentleman arranged for it to be sent to London for examination by George Busk, Schaaffhausen's translator. The specimen itself clearly belongs to the same hominid species represented by the probably male Neanderthal individual, though it is considerably more lightly built and may represent a female. The cranial vault is long and low, and the forehead slopes sharply back from the eyebrows, which are adorned with distinct ridges. The vault protrudes rearward, while the face is large and somewhat projecting, with a wide nasal aperture and backward sweeping cheekbones. The significance of the Gibraltar skull was not lost on Busk, who immediately reported this proof that the Neanderthaler did "not represent... a mere individual peculiarity." The specimen was evidence that the Neanderthaler may indeed have represented a "[r]ace extending from the Rhine to the Pillars of Hercules." "Even Professor Mayer," Busk wrote, "will hardly suppose that a rickety Cossack engaged in the campaign of 1814 had crept into a sealed fissure in the Rock of Gibraltar."

Alas! Busk's shrewd commentary fell on deaf ears. Huxley had taken to task Carter Blake, the secretary of the Anthropological Society in London, for suggesting that the Neanderthal bones were simply those of some poor idiot or hermit who happened to die in the cave. Yet pathology and idiocy (for certain inherited conditions that result in mental deficiency also involve abnormal development of the skull) continued to be favored explanations for the unfamiliar morphology of the Neanderthaler. This was especially true in Germany where the specimen, almost inevitably, became the center of an increasingly bitter controversy. The distinguished and antievolutionary pathologist and anthropologist Rudolf Virchow decided in 1872 that the Neanderthal individual was an aged man who had suffered rickets in childhood, head injuries in middle age, and chronic arthritis in his later years. These factors accounted for his odd morphology; and what's more, Virchow said, the fact that he was able to survive with these disabilities showed that he could not be ancient, for in a presettled society he could not have survived.

It was perhaps inevitable that the Neanderthal specimen, as the only truly distinctive early human then known, should become embroiled in the disputes over evolution itself in the years immediately following the publication of *On the Origin of Species*. But the variety of opinions that it elicited also reflected something else: the nascent science of paleoanthropology was just beginning to feel its way forward. With no other comparable fossils and no existing body of interpretation to provide an analytical framework, it is hardly surprising that almost every possible explanation for the odd appearance of the Neanderthaler was explored in the years immediately following its description. Disease, idiocy, trauma, the outer limit of normal variation, membership

in a species totally disconnected from modern humans—how many more possibilities could there be outside the realm of theology?

Well, one. The one, indeed, that most naturally occurs to (most of) us today. The Neanderthaler could have belonged to a species ancestral to humans, or to a collateral relative. But this idea was totally foreign to the received assumptions of the time, most of which dated back to well before the advent of Darwinism. For years a major concern among anthropologists had been the origin of the human races. Some held that these had diverged from a single origin; others thought that they had been separately formed. While the strict Biblical account of Creation held sway, the idea of a single origin in the Garden of Eden was naturally favored, but as the literal reading of Genesis lost ground in the later nineteenth century, the idea of multiple origins garnered more support. The Dutch science historian Bert Theunissen has pointed out that as Darwinist ideas caught on, both of these perceived possibilities of human racial origins were easily incorporated within an evolutionary context: either humans had diversified from one ancestral species or each race was descended from an extinct nonhuman species. Emphasis was placed on the differences between human races, rather than upon their similarities; and typological notions—essentially of fixed form—ruled the day. This was in fact rather ironic, since even back in Buffon's time it had been permissible to speculate about the transformation of one infraspecific form into another, while it was now only permissible to talk in terms of transformation between species. But the upshot was that anthropologists could with little difficulty fit the Neanderthaler into the spectrum of defined human types as an added category. This was especially so since European scientists were prone to rank various perceived varieties of the human species on a scale of perfection that unsurprisingly placed them at the top. And since it was not uncommonly believed that the races at the top and bottom of the ladder were more dissimilar from each other than those at the bottom were from the apes, the Neanderthal type fit even more comfortably at the foot of this ranking.

Another reason for neglecting the possibility that the Neanderthaler was a human ancestor or collateral relative was that, as in some circles today, in the 1860s the fossil record was not thought to be central, or even particularly relevant, to the problem of sorting out evolutionary relationships. The proof of evolution was sought and found in comparative anatomical and embryological similarities: to a greater or a lesser extent organisms share structural features and developmental sequences, and it is these that reflect and are explained by their common descent. The ebulliently Darwinian German school of morphology, in particular, was based entirely on the use of comparisons among living organisms to elucidate the order inherent in natural diversity; indeed, the dictum of the great German embryologist Ernst Haeckel, that "ontogeny recapitulates phylogeny," virtually made not only the fossil record but the comparative study of adult organisms irrelevant to the clarification of

evolutionary relationships. And indeed, although Haeckel's belief that in its individual development each organism goes through all of the stages through which its antecedent species had passed is not literally true, it is nonetheless quite possible in principle to figure out relationships among extant animals without knowing anything of their fossil record. What fossils do, we now realize, is to both add a unique time dimension to our reconstructions of evolutionary history and enlarge the comparative base available to us. But in the mid-nineteenth century the human fossil record, while accepted as evidence of human ancientness, was simply not associated with the idea of human descent.

Theunissen has drawn attention to one other widely held belief that militated against accepting the Neanderthaler as a precursor of modern humans. From the early years of the nineteenth century onward, the belief gained ground that modern Europeans had not developed in situ, but were the descendants of people who had entered the region from somewhere in central Asia. Originally based on linguistic evidence of similarities between European languages and the more ancient Sanskrit of the Indian subcontinent, this idea gradually came to incorporate notions of race. By the third quarter of the nineteenth century, the so-called "Aryan hypothesis" had been elaborated to a point where it envisioned a late Paleolithic or Neolithic invasion of Europe by agricultural peoples from the south and east. These "superior" invaders supplanted the indigenous hunting peoples, who were assumed to have been wiped out or otherwise to have become extinct. The Paleolithic Neanderthaler, then, could hardly have borne any direct relation to modern Europeans. Paleolithic Europeans were of incidental interest; human ancestry that mattered was to be sought in Asia. So while later finds, notably of two quite complete Neanderthal skeletons at the Belgian site of Spy in 1886, finally persuaded the world that here indeed was a distinct form of archaic human, few even then appreciated its significance. Indeed, quite amazingly, the precise relationship of the Neanderthals to ourselves remains debated to this day.

Antiquarianism Transforms into Archaeology

Even as the notion that, as Darwin put it, "species are the modified descendants of other species" was rapidly gaining favor among biologists, the antiquarians were transforming themselves into archaeologists and in the process establishing beyond doubt the ancientness of the human lineage. They were, moreover, moving beyond this more generalized goal to develop a chronology of the prehistoric human past. In 1865 the English archaeologist Sir John Lubbock published his *Prehistoric Times*, in which he adopted the scheme of successive Stone, Bronze, and Iron Ages already proposed by two Danish scholars, Christian Thomsen and Jens Jacob Worsaae. Lubbock further subdivided the Stone Age into earlier and later periods: the Palaeolithic, characterized by flaked or chipped stone tools, and the Neolithic, in which polished



Side and front views of the "Old Man" cranium found in 1868 in the rock shelter of Cro-Magnon, southwestern France. Scales are 1 cm. DM.

stone tools were used. It was already abundantly clear by 1865 that of all these periods the Paleolithic was by far the longest, and it was not long before it was in turn subdivided.

Progress toward this subdivision surged in the middle 1860s, when the paleontologist Edouard Lartet and a local aristocrat, the Marquis de Vibraye, began to explore the archaeological potential of the caves and rockshelters in the limestone landscape of the Dordogne region of western France. It had been known for years that shaped flints and bone were abundant in the earth filling such sites in the Dordogne, though Lartet's attention had initially been attracted by sites further to the south, such as the rock shelter at Aurignac, southwest of Toulouse, which in 1852 had yielded a large number of human burials in association with an extinct fauna and stone tools.

In 1868 Lartet and the English banker Henry Christy excavated a small rock shelter in Les Eyzies de Tayac, a village in the valley of the Vézère River which was destined rapidly to become the "Capital of Prehistory." At this site, Cro-Magnon (as the rock overhang beneath which a Monsieur Magnon kept his farm implements was known in the local patois), workmen digging fill to construct a road from the newly built railway station into the village had uncovered some human skeletons. Lartet and Christy's investigations revealed that at least five burials, one of an infant, had been made in the rock shelter. These people were of modern form but were associated nonetheless with stone tools and the remains of extinct animals. It was the Cro-Magnon site that gave its name to the first modern people of the Dordogne region and by extension of Europe as a whole.

Between 1865 and 1875 the various parts of Lartet and Christy's great work *Reliquiae Aquitanicae* were published. In this landmark study Lartet and Christy suggested that although Le Moustier, Laugerie Haute, and La Madeleine, three of their sites near Les Eyzies, were clearly of the "age of

simply worked stone without the accompaniment of domestic animals," they did not "possess a uniformity in the production of human industry." Clearly the Paleolithic had to be subdivided. As a paleontologist Lartet understandably tried to do this by means of the animals associated with the tools, recognizing a Cave Bear period, a Woolly Mammoth period, a Reindeer period, and so forth. Archaeologists, however, were unhappy with the idea of categorizing periods of human cultural development on the basis of zoological criteria, and it was not long before the archaeologist Gabriel de Mortillet reworked Lartet's chronology to correspond to the stone tool types that characterized the various periods.

de Mortillet's classification of 1872, enshrined in his great *Le Préhistorique* of 1883, recognized four periods of distinctive stone tool making in the Paleolithic. Each of these was named after the locality in which it was first or best represented. The oldest of these industries, or cultures, was the Chellean (later changed to Abbevillian), named for one of Boucher de Perthe's sites in the Somme Valley. Flint tools of this age included massive handaxes made by knocking flakes off a "core" until a standard shape was obtained. This was followed by the Mousterian, in which tools were fashioned on large flakes that had been detached from a core shaped to predetermine their form. Next came the Solutrean, characterized by incredibly finely worked "laurel-leaf" points. The final period of the Paleolithic was the Magdalenian, when fewer tools were fashioned from stone and more were made of organic materials such as bone and antler. Later editions of de Mortillet's work added the Aurignacian period between the Mousterian and Solutrean (as the first period of the Upper Paleolithic) and inserted the Acheulean following the Chellean. In its essentials, this chronology of the Paleolithic survives today. Despite the general antipathy to Darwin's ideas that reigned in a France still in thrall to the shade of Cuvier, de Mortillet was also an enthusiastic Darwinian and was an early supporter of the idea that the roots of *Homo* were ancient indeed. He it was who coined the term "eoliths" (dawn stones), for the simple tools that he expected "Homo-simius," the human precursor, to have made.

As the complexities of the archaeological record of the Paleolithic were emerging, the earliest evidence of artistic activity by Aurignacian and later peoples was coming to light. As early as 1833 a baton and harpoon made of antler, both decorated with engraving, were found in the cave of Veyrier in Switzerland; and at around the same time an engraving of two deer on a plaque of reindeer bone was recovered from the French cave of Chaffaud. Thought by its discoverers to be Celtic, the Chaffaud piece was recognized by Lartet to be of Paleolithic origin, and he published it as such in 1861, along with an engraving of a bear's head which had been excavated in the cave of Massat in the foothills of the French Pyrenees. At Aurignac, too, engravings on bone had been found; and in 1864 Lartet and Christy published a detailed discussion of this evidence of ancient artistic activity. Objectively, there could be little doubt about the ancientness of such pieces. After all, most of them

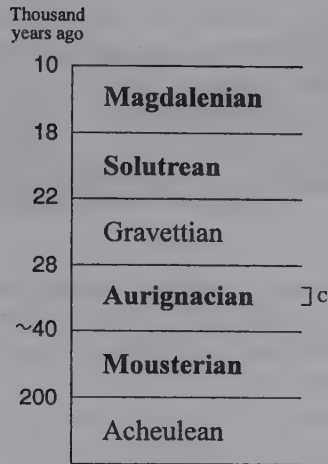


Chart showing the succession of the principal cultures commonly recognized in the European Paleolithic. Names in boldface were coined by Gabriel de Mortillet. Dates shown are approximate. The bracketed symbol "C" on the right-hand side of the chart gives the approximate duration of the Châtelperronian culture. *DS*.

had been found in situ, buried under thick piles of sediment and in association with extinct animals whose representations they sometimes bore. And although the idea of prehistoric art took some time to be absorbed by the establishment, by 1867 the veracity of Paleolithic "portable" art was sufficiently well established that fifty-odd examples of it were placed on exhibit in the great Universal Exposition, held in Paris that year.

Cave art from the Paleolithic took much longer to be accepted, however. The first discovery of decoration inside a cave was that of the spectacular painted ceiling of the cave of Altamira, in northern Spain, by the young daughter of Don Marcelino Sanz de Sautuola. As her father was excavating in the floor of the cave in 1879, searching for prehistoric artifacts, she (who alone could stand upright beneath the low ceiling) looked up and saw in the lantern light the now-famous polychrome representations of bison, horses, and other large mammals. Her father recognized the similarities between these images and the engravings with which he was already familiar from portable art and quickly concluded that the paintings were indeed Paleolithic. Initial reaction to de Sautuola's amazingly insightful publication of this remarkable find was favorable, but in academic circles a reaction soon set in, and Altamira was condemned as a fake by one prehistorian after another. Supporters of de Sautuola were soon in a tiny minority, and it was not until near the end of the century, when corroborating finds began to be made at other sites, that opinion turned in de Sautuola's posthumous favor, and the cave art of the Upper Paleolithic was finally accepted as genuine.



Fragment of reindeer bone from Le Chaffaud, France, showing engraved hinds. Probably of Magdalenian age, this piece was among the first works of Ice Age art to be recognized as such. Scale is 1 cm. DM.

Evolving Notions of Early Humans

While de Mortillet was imagining the nature of the tools that might have been produced by an ancient human precursor (and virulently attacking the authenticity of Altamira), others were conjecturing about the attributes of the creature itself. In the forefront of these was the German zoologist Ernst Haeckel. One of Darwin's most enthusiastic supporters, Haeckel was quite ready to plunge into areas, such as the differentiation of different human types, where the master himself trod gingerly if at all. In his long and highly popular 1868 book *The History of Creation*, Haeckel described and illustrated a highly specific tree of life that ran in 22 stages from spontaneously generated "formless matter" at the root to humanity at the top. The apes occupied little twigs near the pinnacle, but on the trunk beneath mankind lay "Ape-Men." The living apes, Haeckel pointed out, cannot be regarded as ancestral forms to man, but an ancestor there had to be. This "hypothetical primaeval man," "who developed out of the anthropoid apes," had a skull which was probably "very long, with slanting teeth...the hair covering the whole body was probably thicker [than in modern humans]...their arms [were] comparatively longer and stronger; their legs, on the other hand, knock-kneed, shorter and thinner...their walk but half erect." What's more, this rather unattractive beast would have lacked the feature that Haeckel believed set off humanity most clearly from its closest relatives in Nature: articulate speech. The human evolutionary stage of speechless ape-men (following "*Homo stupidus*"!) Haeckel called "Alalus, or Pithecanthropus": a name shortly to become famous in another context.

In his own equally lengthy but more readable contribution, *The Descent of Man*, published in 1871, Darwin himself was a little less exuberant; indeed, despite his title, he was far more occupied by the question of sexual selection (female choice) as a factor in evolution than by the consideration of human descent per se. The fossil record he ignored almost entirely, merely remarking in passing that the Neanderthal skull was "well developed and capacious." He had no difficulty, however, in concluding that the anatomical and

embryological similarities shared by humans and apes were far too numerous to be due to anything but common descent from an ancestor more generalized than any of its living descendants. This ancestor was, according to Darwin, a "hairy quadruped, furnished with a tail and pointed ears, probably arboreal in its habits, and an inhabitant of the Old World."

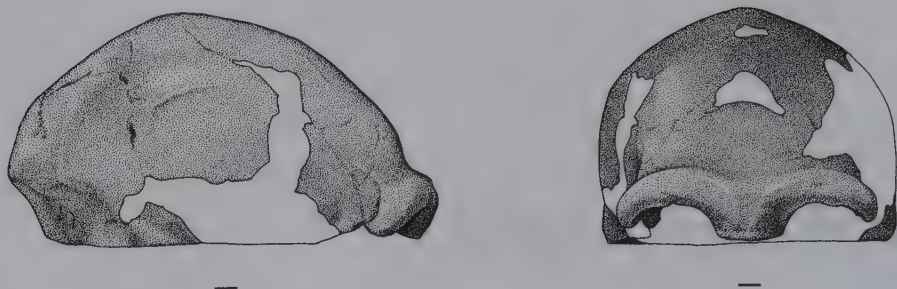
Darwin's argument was a biological one, structured as we've seen around the use of embryological and anatomical comparisons to demonstrate the commonality of descent between human beings and other living things. It is thus hardly surprising that in his consideration of human descent he did not look to archaeological information to flesh out the picture of our species' past. de Mortillet had no such reluctance, however. He believed that cultural evolution was intimately tied in with the later part of the history of human divergence from "lower" forms, and he gave the name *Anthropopithecus* to a hypothetical human ancestor that had lived late in the Tertiary Period. No fossils of such an intermediate ape-human ancestor were known; but to de Mortillet a graded series had to have existed between an apelike ancestor and modern humans. In his later works he came to see the Neanderthals, by then associated with the "Mousterian" culture, as a stage in this process that still bore some hints of ape ancestry. And just as he imagined that in the past a continuous succession of steadily more human species had existed, he perceived a constant linear sequence of cultures throughout the Paleolithic, each one giving rise to the next. So, although the idea that the Neanderthal fossil represented a form ancestral to modern humans was the one theoretical possibility that was not entertained by any of the anatomists who commented on the specimen, the archaeologist de Mortillet had hit on a theme which was to invoke an abiding fascination on the part of paleoanthropologists: one that runs deep in their science to this very day.

CHAPTER 3

Pithecanthropus

During the 1870s and 1880s the Paleolithic archaeological record continued to accumulate much more rapidly than the human fossil record. An occasional modern-looking human skull turned up at this or that ancient archaeological site, but apart from the discovery in 1886 of two nearly complete Neanderthal-like adult skeletons in the Belgian cave of Spy, no new archaic human fossils were discovered during this period. The Spy finds were of the greatest importance both because they confirmed that the original Neanderthaler was no aberration and because they were found in an undisturbed archaeological context that established, beyond any doubt, both the great antiquity and the Mousterian cultural association of these early humans. The describers of the Spy specimens, Julien Fraipont and Max Lohest, considered that these humans were greatly “advanced” beyond the apes and must have been descended from forms more apelike yet, but despite this evolutionary viewpoint they ultimately concluded that they represented a “human race.” Thus it was that the 1890s arrived with no accepted physical evidence for the remote “apish” human ancestor whose existence more and more scientists were willing to hypothesize if not to recognize.

One of the many reasons for the sparseness of the nineteenth-century human fossil record was that all of the early human remains that composed it were incidental finds. They had turned up as byproducts of quarrying or construction, of fieldwork by geologists, or of the excavations of antiquarians and prehistorians in search of artifacts. Despite the paleontological expertise of Edouard Lartet, who had done as much as anyone to establish human antiquity, no really ancient human fossil had ever been found as the result of fossil collecting in the paleontological tradition. Virtually every early human specimen then known had been recovered from sediments that had collected in cave mouths; none had come from the layers of sedimentary rocks that normally yield fossil bones. Few cave sites contain deposits that are more than several tens of thousands of years old; only in the strata that compose the general landscape are truly ancient fossils to be found. So to find truly ancient human fossils in the scientific climate of the late nineteenth century required a unique kind of inspiration.

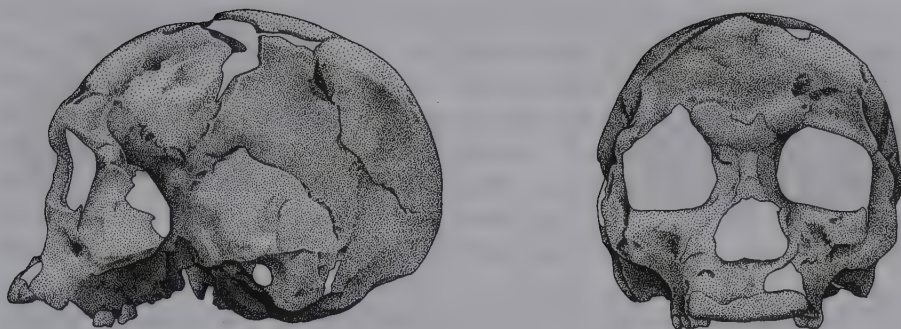


Side and front views of one of the Neanderthal crania (Spy 1) from the Belgian site of Spy. Scales are 1 cm. *DM.*

Java Man

Nobody knows exactly why Eugene Dubois, a young Dutch anatomist and physician, should in 1887 have sailed for the Dutch East Indies with the avowed intention of finding the remains of fossil man—although he certainly seems to have been fired up by a lecture he had heard in medical school by the charismatic Ernst Haeckel (who had “predicted” the existence of a fossil ape-man and had urged exploration for it in the “bone caves” of the Malay archipelago). Dubois, though a keen naturalist from childhood, had had a relatively conventional education in biology and anatomy: an education, what’s more, in the Germanic tradition, which tended more perhaps than any other to eschew the fossil record in documenting evolution. It is known that Dubois was uncomfortable in his position as an instructor of anatomy at the University of Amsterdam, and his practical reasons for trying his luck at finding human fossils in the East Indies rather than elsewhere are clear enough, but there is nothing known about his background that even comes close to explaining why he should have thrown up everything—his job, his prospects as an anatomist—to become the first human paleontologist, especially since at the time his mother country had hardly anything in the way of a paleontological tradition.

Nonetheless, at some point Dubois became a convinced Darwinian, and of the ilk that rejected the Haeckelian notion that fossil evidence for human evolution was not essential (despite Haeckel’s prediction that it would be found). Dubois felt, deeply, that the course of human evolution could only be demonstrated and described through fossils, and he conceived a mission to find them. In view of this it is perhaps odd that Dubois’s view of the Neanderthal skull and others like it was utterly conventional. He saw no hint in these fossils that they might be precursors to modern humans. Even if they were not pathologically deformed, he thought, these specimens showed only that a primitive race of human beings had existed. Nonetheless, in this conventional view we can see a key to Dubois’s unconventional actions: Neanderthals could not be pre-humans because, as received wisdom indicated, people had arrived in Europe



Side and front views of the fossil modern human skull found at Wadjak, Java. Scales are 1 cm. DM.

only *after* becoming fully human. Clearly, then, to find the precursors of *Homo sapiens* it was necessary to look outside Europe.

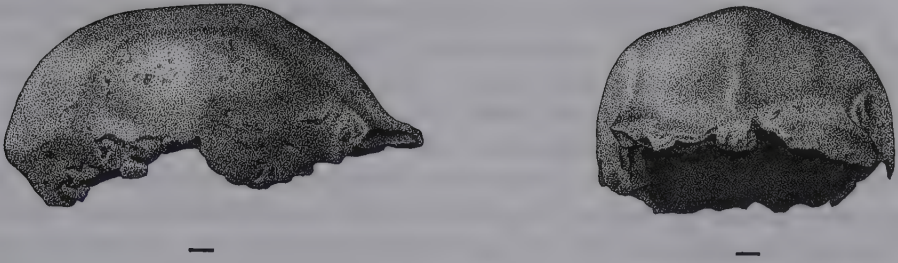
Where? Darwin's candidate as the cradle of mankind had been Africa, tropical home to two of the three great apes then known: the chimpanzee and gorilla. But Dubois had no private means; and wherever he was to go, he needed employment. This is why he eventually signed on as a medical officer in the Royal Dutch East Indies Army, which provided him with a means of getting, at government expense, to the region inhabited by the third great ape: the orangutan. And the orangutan had figured largely in many early theories about human origins and humanity's place in nature. Dubois's reasons for choosing the Dutch East Indies as the sphere of his operations were thus not solely financial. These islands were tropical, and it was generally agreed that the human ancestor had lived in the tropics. Their extinct fauna, insofar as it was known, was thought to resemble that of India, where as early as the 1870s fossil apes had begun to be found in sediments associated with the building of the Himalayas. In Dubois's day this material consisted of parts of an upper jaw of a form then known as *Palaeopithecus sivalensis*. This form was thought by its describer Richard Lydekker to be a relative of the chimpanzee, and in 1886 a tooth indistinguishable from an orangutan molar was also found. What is more, the East Indies were, of course, the home of the orangutan and of the lesser apes, the gibbons and siamangs. If humans were descended from apes, then a part of the world with both living and presumed fossil apes offered enticing prospects for finding a human ancestor. And finally, from the point of view of discovery, the calcareous rocks of Sumatra and other East Indian islands were known to be riddled with caves—just like the sites in which the European fossil humans had been found.

Still, Dubois's move was a huge gamble, and it is truly remarkable that it paid off. At first it didn't, although his initial cave-exploration efforts in Sumatra were rewarded with an impressive collection of fossil bones of living

species, on the basis of which he was able to gain government support for his fieldwork. But continuing explorations in Sumatra were disappointing, and in 1890 Dubois transferred his attentions to Java, where a fossilized human skull had been found in a rock shelter at Wadjak, in the eastern part of the island. The skull was that of a modern human, although Dubois concluded that it differed sufficiently from those of the current inhabitants of Java to represent a distinct earlier population. Cave investigations continued to be unexciting, however, so Dubois directed his workforce—a gang of convicts under the supervision of two army corporals—to excavate in open-air geological deposits already known to yield mammal fossils, often those of extinct species. In November 1890 he found his first human fossil bone, among those of many other vertebrates, at a site called Kedung Brubus. The specimen was an unimpressive fragment of lower jaw, with only one premolar tooth and the socket of a canine. Dubois wasn't able to make much of it, and neither has anyone since. But before long, better material was at hand.

In 1891 Dubois began to investigate some alternating beds of sandstone and volcanic rocks near the village of Trinil, on the banks of the Solo River in central Java. Unlike conventional paleontologists, who—except when collecting very tiny fossils—generally look for bones that are eroding out of exposed sediments and excavate only to recover specific fossils, Dubois's crew proceeded like archaeologists, digging trenches in the ground. At Trinil the convicts dug a vast pit, forty feet across and eventually fifty deep. The many fossils found were packed in teak leaves and dispatched periodically to Dubois, who spent most of his time at his base in Tulungagung, a considerable distance away. Unfortunately, this approach did not permit precise localization of where each fossil was found—a problem that came back to haunt Dubois and that continued to bedevil paleoanthropology in Java long after his time. Still, the digging was effective: in September 1891 a hominoid molar tooth was found (Hominoidea is the name of the zoological superfamily that contains humans and the apes), and in the next month a skullcap emerged. This was broadly equivalent in completeness to the original Neanderthal specimen, though its braincase was much less capacious. Dubois first reported these remains as fossil chimpanzees, having concluded that they resembled neither gorillas nor orangutans. But he soon changed his mind.

The next year, after the floods of the rainy season had subsided, workmen found a femur in an extension trench at Trinil. It was reportedly recovered from the same stratigraphic level as the skullcap and tooth, but some distance away—variously said at different times to be fifteen, twelve, or ten meters. Though it bore a large pathological excrescence, this femur was just like that of a modern human, and its possessor had clearly walked erect. Since a reappraisal of the cranial vault had shown it to be too capacious for any living ape, Dubois concluded that what he had before him were the remains of an apelike man rather than a manlike ape. In homage to Haeckel he gave it the name *Pithecanthropus erectus*, “upright ape-man.” Haeckel returned the compliment



Front and side views of the original Trinil *Pithecanthropus* skullcap discovered by Eugene Dubois in 1891. Holotype of *Homo erectus*. Scales are 1 cm. DM.

by wiring Dubois "congratulations to the discoverer of *Pithecanthropus* from its inventor."

Somewhat as in the Neanderthal individual, the eyes of *Pithecanthropus* were overhung with ridges. The vault of the rather smaller skull was long and low (yet higher than that of an ape) and sharply angled at the rear. The brain-case was composed of thick, heavy bone. Dubois estimated that the individual's brain volume had been around 1,000 ml. This is at the extreme lower limit for modern humans, who average about 1,400 ml (as do Neanderthals, but Dubois declined to compare his specimen with Neanderthal and Spy because he thought them pathological, as well as variants of modern humans). In later years Dubois dropped his brain volume estimate to 900 ml; modern calculations place it at 940 ml. For comparison, chimpanzee brains average around 400 ml and those of the much larger gorilla, about 460 ml. Brain size is, of course, to some extent dependent on body size, but Dubois figured on the basis of the femur that the stature of his early human had been similar to that of modern Europeans. As to the age of his *Pithecanthropus*, Dubois hazarded from the huge associated fauna that the specimens dated from the late Pliocene or early Pleistocene, intermediate between the Indian Siwalik fauna and the human specimens known from the late Pleistocene of Europe.

Was this upright ape-man the human ancestor he had been seeking? In a lengthy description published in 1894, Dubois argued that it was impractical to classify *Pithecanthropus* either in the human genus *Homo* or as an ape. Instead it stood between them, as the notion of evolution suggested some creature must have done. He proposed that a gibbonlike ancestor had given rise to the extinct Indian "chimpanzee," which had in turn evolved into *Pithecanthropus erectus*, whence *Homo sapiens* (including the Neanderthals) had sprung. This suggested that major anatomical shifts had occurred between each of these successive stages, but Dubois saw no problems with jumps of this kind. Furthermore, his new species suggested to him that Lamarck and Darwin had been right to conclude that an upright bipedal way of walking had been the first new adaptation to characterize the lineage leading to human beings. Only later had such traits as manual dexterity and a large brain been acquired.

But while the femur showed undoubted evidence of human bipedality, the skullcap was different, retaining vestiges of the "ape-type" in its skull; thus, although *Pithecanthropus* had certainly advanced some way toward human status, it could not yet be classified in Hominidae, the family of mankind. And while he finally decided to place it in its own family, Pithecanthropidae, Dubois continually returned in his description to comparisons with the chimpanzee and more particularly the gibbon. This "lesser" ape brachiates through the trees, swinging arm over elongated arm. But on its rare descents to the ground, it walks bipedally. This observation deeply affected Dubois and led him down a blind alley into which many others followed him.

This, then, was the message that Dubois took with him to Europe when he returned there in the summer of 1895. During the late Pliocene or early Pleistocene (and in those days nobody knew how long ago that was; Lyell had estimated in 1863 that the Pleistocene had lasted 800,000 years, while by 1900 the English geologist W. J. Sollas had reduced it to half this) an upright being intermediate between ape and man had lived in Java. Although Dubois's 1894 description of his *Pithecanthropus* fossils had been published in remote Batavia (now Jakarta), and as a pamphlet rather than in a recognized journal, news of his find preceded his return to Holland. Most scientists' initial reaction was to question the association between the skullcap and the femur. Some critics dismissed the cranium as that of an ape (possibly, according to some authorities, a giant gibbon) while attributing the femur to a modern human. Others, particularly in England and Ireland, were willing to accept the skullcap as human, although of a rather low order. The Dublin anatomist Daniel Cunningham, for one, was prepared to see *Pithecanthropus* as a form which had given rise, via the Neanderthals, to modern humans, though he regarded the femur as fully modern. And in America the famous paleontologist O. C. Marsh concurred in detail with Dubois's conclusions. At the beginning, however, the poorly established physical association between the femur and the skullcap was seen as undermining Dubois's interpretation.

Once again, we have to bear in mind that this debate was conducted in the absence of any substantial body of comparative material. The idea that the Neanderthals were not simply an odd ancient race of modern humans was still foreign to most points of view, which meant that the *Pithecanthropus* materials were all that stood between humans and apes. And to many the skullcap and femur appeared to tell different stories, so that to exploit the doubt over their association was also to simplify their interpretation. As important, in the closing years of the nineteenth century there was no coherent body of expectation against which any new fossil could be tested. Agreement was reasonably complete that descent with modification was indeed the explanation for the diversity of living organisms, but opinions varied greatly on how evolution actually worked. Darwin's mechanism of natural selection had its adherents, but by no means did all biologists subscribe to it. Besides, despite having called his book *On the Origin of Species*, Darwin had barely considered the question raised in

its title. Natural selection as proposed by Darwin dealt with the morphological transformation of lineages, and this, depending on your point of view, is not quite the same thing, or is not the same thing at all. Even such staunch supporters of evolution as Huxley had taken Darwin to task for concentrating so singlemindedly on the slow accretion of small changes. Echoing the sentiments expressed in the letter quoted earlier, in reviewing Darwin's book Huxley wrote that "Mr Darwin's position might...have been even stronger than it is, if he had not embarrassed himself with the aphorism 'Natura non facit saltum' [Nature makes no leaps]...nature does make jumps now and then, and a recognition of the fact is of no small importance." Huxley echoed the view of many, while others clung to Lamarckian ideas and the notion that evolution was somehow goal directed. Small wonder, then, that with theory providing no consistent guide to the interpretation of the scantiest of fossil records, explanations of Dubois's *Pithecanthropus* multiplied rapidly.

It has often been reported that these interpretations were generally unfavorable to Dubois's point of view and that it was this negative reaction that caused Dubois, in the years after 1900, to withdraw himself—and later his fossils as well—from the fray. However, Bert Theunissen convincingly showed some time ago that Dubois was much more successful than usually supposed in winning converts to the idea that *Pithecanthropus* was an ancestral human form, or one that was at least close to human ancestry. Between 1895 and 1900 Dubois had traveled widely in Europe, showing off his specimens at various international congresses. On viewing the original specimens, many of his colleagues turned out to be prepared to modify their ideas. Most eventually accepted that the femur and the skullcap of *Pithecanthropus* were indeed associated, and virtually all agreed, upon seeing how thoroughly the bones were fossilized, that they were very old indeed. Not that opposition to Dubois's interpretation of his fossils was entirely lacking; Virchow, for one, loudly proclaimed that the remains were those of a giant gibbon, though this interpretation may have owed less to scientific considerations than to his vicious quarrel with Haeckel, who supported Dubois with equal energy. But even those who saw in *Pithecanthropus* a more apelike or a more humanlike form than Dubois did agreed that here was a manlike ape or an apelike man. And in his turn Dubois found support for his theories in the fact that both extremes of opinion were represented. A few authorities held out the possibility that the specimen was pathological, or that it merely represented an extinct human race, but eventually they found themselves in a small minority.

Changing Views of the Neanderthals

Given the stir created by the new material from Java, it was inevitable that the Neanderthals should once again come under scrutiny. And although Dubois himself never shifted from the idea that these were simply an extinct race of *Homo sapiens*, other scientists who accepted that *Pithecanthropus* lay on

or close to the line of human descent now found it easier to envision the Neanderthals as a later stage in the same process. Influential among them was the German anatomist Gustav Schwalbe, who produced long monographs on both *Pithecanthropus* and Neanderthal in the years around the turn of the twentieth century. Schwalbe perceived a morphological series from the apes to *Pithecanthropus* to the Neanderthals (which, ignoring King's earlier name, he christened *Homo primigenius*) to *Homo sapiens*. He considered the Neanderthals closer to *Pithecanthropus* than to modern humans. As his ideas developed Schwalbe came to see this series as a line of descent, reflecting a consensus that was gathering strength, particularly in England. In the end, Schwalbe's minutely documented analyses played a critical role in getting the Neanderthals accepted as a distinct form of early human—an acceptance that was also helped along by the decline of the Aryan theory in the closing years of the nineteenth century and by the gradual disappearance of the single/multiple origin dispute in the discussion of human races.

But Schwalbe's intense interest in *Pithecanthropus* seems to have had a more direct and unintended effect on Dubois himself. For, displaying a mindset that endures to this very day, Dubois seems to have perceived his intellectual capital disappearing as exegeses of his fossils came out under the signature of other scientists. Eventually he withdrew the bones from scientific access (they remained locked away until 1923). During this period he devoted himself to a series of studies of comparative brain size in mammals, which he had already begun with the aim of showing that *Pithecanthropus* indeed stood intermediate between the apes and mankind. Adhering to a notion of evolution by abrupt change, and of an inner urge to "perfectionism," as opposed to the gradual change in response to external factors postulated by Darwin, Dubois concluded late in his career that mammalian brain evolution had occurred via a series of sudden doublings in size, each due to an additional division of the primordial brain cells. These had proceeded such that, compared to body volume, apes (including gibbons) had one fourth the amount of brain that humans have; the majority of mammals ("Ruminants, Cats, Dogs, etc."), one eighth; rabbits, fruit bats, and various other forms, one sixteenth; mice, moles, and leaf-nosed bats, one thirty-second; and shrews and "common Small Bats" (representing the most primitive mammals), one sixty-fourth.

In this series, one stage was glaringly missing: the stage between the apes and man, with a brain one-half the relative size of the human one. It was in this position that a form transitional between the apes and man would have to fit. But while the femur seemed to indicate that *Pithecanthropus* had been as large as modern humans, the skullcap had held a brain not one-half but about two-thirds modern size. There was a way out, though: if *Pithecanthropus* had boasted gibbonlike body proportions, with relatively short legs and a large thorax, it would have been much heavier than a human with a femur of similar length. Using the greater body weight that such proportions would yield, the brain:body ratio of Dubois's "Java Man" fell neatly into the doubling series.

It was thus in defense of his original conclusion that *Pithecanthropus* was transitional between apes and humans that Dubois claimed gibbonlike characteristics for it. But in this construct the ape ancestor became not a great ape but a lesser one; and as he grew older, the gibbon hypothesis took on a life of its own. By 1935, for example, Dubois felt able to assert that *Pithecanthropus*, although an upright walker, had upper limbs that “still exerted locomotor functions...in a similar manner as in the Gibbons”—which, as we’ve seen, are highly specialized arboreal armswingers. By this time Dubois was thoroughly out of step not only with evolutionary theory and a growing body of knowledge about brain structure and function, but also with advancing interpretations of the human fossil record. After about 1900, then, he contributed little to the mainstream of debate on human evolutionary history—even though he himself had done more than anyone else to spur that debate initially. Fixating on his *Pithecanthropus*, he refused to acknowledge the significance of other near-human fossils that were coming to light.

CHAPTER 4

The Early Twentieth Century

In 1900 three investigators independently rediscovered the principles of inheritance first enunciated 34 years earlier by the Moravian cleric Gregor Mendel in an obscure local journal (although Darwin apparently had a copy in his library—with the pages uncut). Concepts of inheritance up to that time had been vague and sometimes Lamarckian. Most of them involved some idea of “blending,” since it was widely recognized that in sexually reproducing species offspring, while not identical to either parent, tend in many ways to resemble them both. It was Mendel’s great insight to study the transmission of traits that did not behave this way. Growing flowering peas in his monastery garden, he carried out breeding experiments on plants that bred true for traits that existed in two alternative forms: stature (tall or short), seed color (green or yellow), and so forth. Mendel elegantly showed that such traits are specified by inherited factors (which we now know as genes) that exist in pairs (alleles). One allele of a pair (say, tall) might be dominant over the other (short). The other (recessive) allele would not be expressed in its presence, but the two discrete alleles were still present in each individual, and each had an equal chance of being passed along to the next generation. Further, each discrete trait (stature, seed color) might turn up in combination with any other such trait; no two were transmitted together.

Today we know that genes behave this way because each individual possesses a double set of chromosomes, one inherited from each parent. Along these the genes are arranged more or less sequentially. Each chromosome of a pair carries one set of alleles. The traits Mendel chose to look at were all carried on different chromosomes, and each was determined by only one gene. Either he was lucky—very lucky—or he had a very shrewd intuition. In most cases, as the fact that offspring tend overall to look a bit like both parents suggests, most physical characters are influenced by more than one gene—usually on different chromosomes—while most genes affect more than one character. And it turns out that the genome is in fact mind-bogglingly complicated, with genes as structural elements far from the whole story. Still, Mendel’s simple

laws were an absolutely essential prelude to understanding the complications inherent in genetic transmission.

Mendel's acute observations languished unappreciated for over three decades, during which other notable advances in the science of inheritance were nonetheless made, notably the anti-Lamarckian demonstration by the German biologist August Weissmann that there was a total separation between modifications of the physical being and of the material of inheritance. But the rediscovery of Mendel's principles unleashed an astonishing burst of activity in the nascent field of genetics. If inheritance was discrete—and even if multiple genes were usually involved—the patterns of heritability could be modeled mathematically and the study of inheritance could finally be put on a scientific footing. And if evolution was the sum total of perturbations in the transmission of genetic information between generations, here was a mechanism by which evolutionary phenomena could—indeed, must—be explained. So, even though Darwin and his fellow naturalists such as Wallace had been perfectly able to identify and describe the basic phenomena of evolution in the total absence of an accurate notion of how inheritance worked, genetics suddenly appeared to many to be the key to unraveling the mysteries of natural diversity. And although it took several decades for the systematists, paleontologists, and geneticists to come together on this issue, when they did so it was to have profound implications for the future of evolutionary biology.

Genetics and Species

Perhaps paradoxically—but perhaps not, since it provides the starting point for all excursions into the mechanics of change in gene pools—just about the first thing a budding paleoanthropologist is taught nowadays in courses on evolutionary change is the so-called Hardy-Weinberg Principle. First adumbrated in the early years of the twentieth century, this principle is a mathematical demonstration of the fact that the distributions (otherwise known as frequencies) of alleles within a freely interbreeding population of organisms should remain constant from one generation to the next. It is, then, a demonstration of stability, not of changeability, and in later decades it became backed up with a great deal of literature on the subject of genetic homeostasis: the inertial tendency of populations not to change. Still, it is as noted the launching pad of the science that we know nowadays as population genetics, whose practitioners usually regard themselves as evolutionary biologists.

Evolution, of course, involves change, and the big question for population geneticists, as for others, is: How does such change occur? Translated to population genetics terms, Darwin's ideas of natural selection involve gradual shifts in gene frequencies within populations, as favorable genes or gene combinations spread from generation to generation at the expense of less favorable ones. But as people, like dog breeders, selecting for longer legs or shorter muzzles or whatever, had known long before evolutionary ideas had ever taken shape,

by simply shifting gene frequencies you can neither produce true anatomical innovation (you are restricted to producing variations on existing themes), nor can you produce new species. Yet evolution depends both on anatomical change and on the production of new species, and at the end of the nineteenth century the relationship between these two different things remained far from clear. As, to be quite frank, it still does.

To begin with species, as early as 1865 the French naturalist Pierre Trémaux had lamented that "of definitions of species there are as many as there are naturalists;" and this is not a situation that has materially changed in the years since. But Trémaux also put his finger on the crux of the situation, remarking as follows: "Two principal notions have served to define the species: resemblance between individuals and ability to reproduce....[T]he first of these conditions...is...the consequence of the second." This comment holds with equal force today: despite a plethora of formal definitions of what species are, species are still usually viewed as reproductive communities composed of individuals who more or less resemble each other and who are at least potentially able to interbreed among themselves while being unable to do so (or at least to do so efficiently) with members of other such communities. Trémaux was quite right to point out that it is because of their common genetic heritage that the individuals composing a species look similar, but it is nonetheless true that (especially in paleontology) it is almost invariably on the secondary criterion of similarity that we recognize individuals as belonging to the same species. Even among living organisms, let alone among fossils, there are vast problems both in principle and in practice of recognizing exclusive or inclusive reproductive communities, and it is essentially because of these problems that there are still as many definitions as naturalists. But while at least in theory we can recognize species from some aspect of resemblance when we look around us at the living world (though, remember, Darwin himself had had trouble with this), under strict Darwinian tenets we can't do that in the fossil record unless we look only at single slices of time. For via slow, gradual change under the guiding hand of natural selection, Darwinian species are expected to transform themselves out of existence. Reproductive continuity stays unbroken over the millennia, but anatomies nonetheless change, eventually greatly.

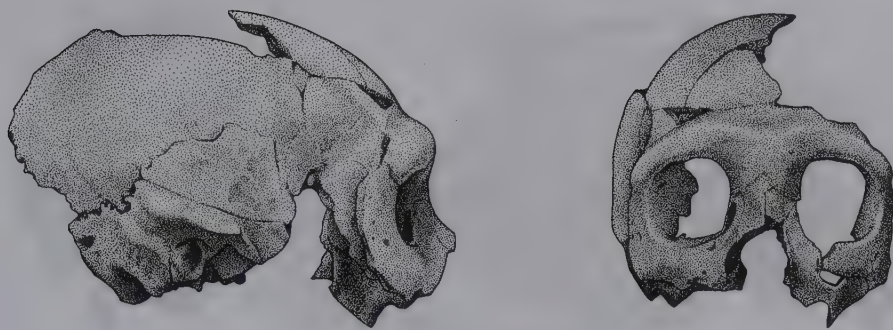
The alternative view, one that was quite popular during the late nineteenth century when natural selection was not greatly in vogue, is to see species as maintaining their identities in time as well as in space. If we do this, we have to be able to explain how one species is able to transform itself into another in a rather short space of time—so short that the likelihood of our picking up the event in the fossil record is negligible. One way of doing this seemed almost self-evident from the work of the geneticists. It had long been known that while most individuals in a population differed from each other only in minor ways, occasionally a "sport" might pop up that was quite different from the norm. Following his rediscovery of the "particulate inheritance" of Mendelian

genetics, the Dutch botanist Hugo de Vries showed that spontaneous changes or "mutations" in an allele could account for innovations of this kind. He also took this idea further, and in 1901 he proposed that new species arose in a similar manner, by sudden steps involving change in one major character or set of characters—an idea of speciation that was rapidly endorsed by many other influential geneticists. What's more, the Mendelians rapidly became more or less unanimous in identifying mutation pressure—the rate at which mutations occurred—as the driving force behind evolutionary change.

This new influence tended to distract attention away from other considerations relating to the origin of species, and it also set the scene for a rift to develop between the geneticists and the more traditional naturalists, systematists, and others. The geneticists, while rapidly developing a body of theory to cope with the obvious fact that inheritance was in most cases more complex than Mendel's simple rules suggested, nonetheless concentrated on the role in evolutionary innovation of discontinuous characters (for example, stature in peas). The naturalists, on the other hand, many of whom were becoming more inclined to accept natural selection, emphasized the importance of continuously variable characters (such as stature in humans) in the evolutionary process. The paleontologists did not contribute materially to this debate, in which they simply tended to take one side or the other: among the paleoanthropologists, Dubois, for instance, supported the mutationist viewpoint of his countryman de Vries, while many others inclined to gradualist interpretations of evolutionary change.

The Hominid Fossil Record Grows

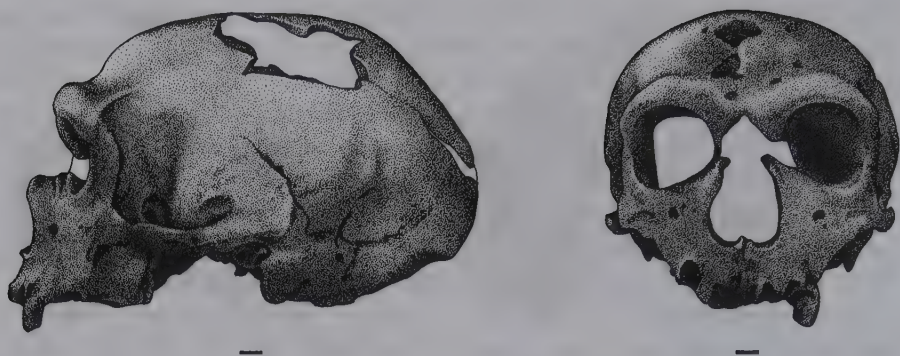
It was in this rather unsettled climate of evolutionary opinion, during which most of those interested in human evolution favored Lamarckian notions and natural selection was still largely out of fashion, that the human fossil record continued gradually to accrete in the early years of the twentieth century. New finds continued to be made by archaeologists or by accident, for few scientists followed in Dubois's footsteps and actually went in search of human fossils, especially after a German expedition under the leadership of Margarethe Selenka spent 1907–08 at Trinil without finding any additional human specimens. This expedition was not without its successes, though, for it did collect many nonhuman vertebrate fossils. Dubois himself had paid little attention to his own enormous assemblage of such material following his return to Europe; indeed, his collection remains incompletely studied to this day. So it was particularly important that study of the Selenka materials confirmed the age of the Trinil fauna as Early or Middle Pleistocene, even though this complicated the evolutionary picture somewhat. At that point the Neanderthals were considered to be of Middle Pleistocene age, antedating as they did the Cro-Magnon types of the Late Pleistocene; if both Neanderthals and *Pithecanthropus* were of Middle Pleistocene age, how could the latter be



Front and side views of Krapina cranium C, one of many Neanderthal fossils found at that Croatian site around the turn of the twentieth century. Scales are 1 cm. DM.

ancestral to the former? This puzzle was to go unsolved for some time, even as the view gained credibility that *Pithecanthropus* and the Neanderthals stood in the direct line of human descent, or at least represented stages in that line.

But it was not to be unsolved for long. Between 1908 and 1911 the French cave sites of La Chapelle-aux-Saints, Le Moustier, La Ferrassie, and La Quina all yielded up complete or multiple skeletons of Neanderthals, which at last provided an opportunity to appraise the entire bony anatomy of this early human form. These complemented a series of less complete Neanderthal remains that had been excavated in the Croatian cave of Krapina between 1899 and 1905, a fragmentary braincase and other materials found at the German site of Ehringsdorf in 1908, and various other bits and pieces found over the first quarter of the century. For a whole variety of reasons it was the skeleton of the “old man” of La Chapelle, voluminously published by the influential French paleontologist Marcellin Boule, which became the Neanderthal archetype. And Boule was dead set against viewing the Neanderthals as anything but an offshoot of the human lineage that had died out without issue. Anatomically, Boule claimed, the Neanderthals had possessed divergent big toes (hence grasping feet on which, moreover, weight was borne, apelike, on the outer edges), a slouching posture, bent knees, short and thick necks, and inferior brains. What’s more, Boule believed that modern human forms already existed at the time of the Neanderthals (a notion known as the “presapiens” hypothesis). He also pointed out that in France the Mousterian (or Middle Paleolithic) stone tool-making tradition of the Neanderthals had been rather abruptly replaced by the Upper Paleolithic tool assemblages associated with modern human types. This suggested to him that the Upper Paleolithic had been developing elsewhere for quite some time, and he took this as further evidence that the Neanderthals were but a side-branch in human evolution. Boule was quite happy to accept the Neanderthals within the genus *Homo*, as

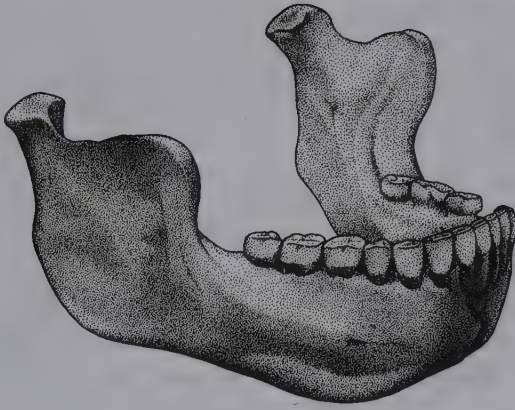


Front and side views of the cranium of the "Old Man" of La Chapelle-aux-Saints, Corrèze, France. Scales are 1 cm. *DM*.

Homo neanderthalensis, but, as he wrote in 1913, in the final part of his long monograph on the La Chapelle-aux-Saints skeleton, he saw a huge "contrast with the... Cro-Magnons, [who] with their more elegant bodies, finer heads, large and upright foreheads... manual dexterity... inventive spirit... artistic and religious sensibilities... [and] capacities for abstract thought were the first to deserve the glorious title of *Homo sapiens*!"

One is supposed not to write Whiggish history, in which figures of the past are measured by their importance in contributing to today's orthodoxies (and indeed, not all of my own opinions diverge too far from Boule's). But, quite apart from Boule's poor opinion of *Homo neanderthalensis*, I have to confess that, try as I may, in reading his 1911-13 monograph I cannot avoid total incredulity at his cavalier treatment of *Pithecanthropus*. In his lengthy consideration of the larger picture of human descent, in which he invoked the names of virtually every fossil primate then known, including such spectacularly irrelevant forms as the recently extinct Malagasy lemurs *Megaladapis* and *Archaeolemur*, Boule granted *Pithecanthropus* hardly more than a passing mention. He was particularly fond of pointing out that physical resemblance was not necessarily proof of phylogenetic descent. Boule had used this weapon with great effect to exclude the Neanderthals from the direct human lineage, and now he employed it once more to exclude *Pithecanthropus* from any human affinity whatever. According to Boule *Pithecanthropus* was, as Virchow had suggested sixteen years earlier, a giant gibbon. It was necessary to look elsewhere for early humans, and Boule had two suggestions.

The first of these was *Homo heidelbergensis*, a species created in 1908 by Otto Schoetensack for a lower jaw that had been found in a sand quarry at Mauer, near Heidelberg. By this time most scientists had come to accept the sequence of four glacial advances during the Pleistocene proposed in 1894 by the Scottish geologist James Geikie. These cold "glacials" had been separated by three "interglacial" phases of milder climate. On the basis of its associated fauna, Schoetensack assigned the Mauer specimen to the Lower Pleistocene,



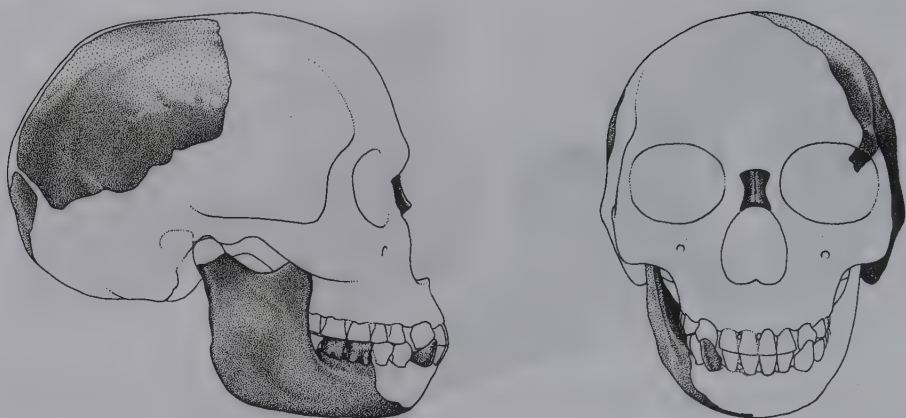
The mandible found at Mauer, Germany, in 1908. Holotype of *Homo heidelbergensis*. Scale is 1 cm. DM.

and specifically to the first interglacial period. This made it undisputably earlier than any other human fossil known from Europe. Schoetensack looked upon the specimen as a precursor of the geologically younger Neanderthals, and Boule generally concurred. For while he considered the teeth to be just like those of modern humans, the jawbone itself was in his view apelike. To Boule the ensemble, though inadequate for definitive analysis, was a potential ancestor for *Homo neanderthalensis*. In contrast, his candidate for the honor of modern human ancestry was *Eoanthropus dawsoni*.

Dawson's Dawn Man

Across the English Channel, interest had lately burgeoned in the possible existence of truly ancient humans of modern type. In 1910 the influential anatomist Arthur Keith restudied a modern-looking human skeleton that had been found in 1888 at Galley Hill in southern England, in deposits of early Pleistocene age. This later turned out to be an intrusive burial that was much younger than the deposits into which it had been interred, but especially with the discovery of what seemed to be a similar association at Ipswich in 1911, Keith came to accept the apparent combination of modern anatomy with great antiquity. It was but a short step from this to rejection of the Mauer specimen and the Neanderthals as members of the direct line of human descent. For if the evidence from Galley Hill was to be believed, these fossils had coexisted with people of modern kind. By the end of 1912 Keith was strongly committed to this view. And then the Piltdown fossils were announced.

As early as 1908 workers digging in a gravel pit at Piltdown, in Sussex, handed some fragments of a thick human skull to Charles Dawson, a local lawyer and amateur paleontologist. Over the next year or two various other



Front and side views of the Piltdown "skull," as reconstructed by Arthur Smith Woodward in 1913. Scales are 1 cm. *DM*.

bits and pieces came into Dawson's hands. In 1912 Dawson gave these fragments to Arthur Smith Woodward, the Keeper of Geology at the British Museum (Natural History) (as it then was) and a leading expert on fossil fish. Smith Woodward joined Dawson and the Jesuit paleontologist Pierre Teilhard de Chardin in working at the site, and together the trio found more bits of cranium, together with part of the right half of an apelike lower jaw, assorted mammal fossils and a few crude stone tools. The fauna seemed to suggest an early Pleistocene or even a late Pliocene age for Piltdown: an estimate that later gained apparent support from geological correlations. Late in 1912 Smith Woodward pieced the various bits and pieces together in a reconstruction of the skull. This was a rather bizarre-looking affair with an ape's jutting jaw and a high humanlike braincase of some 1,070 ml capacity, thus somewhat smaller than typical of modern humans. Just before Christmas Smith Woodward unveiled this marvel, which he named *Eoanthropus dawsoni* ("Dawson's dawn man"), at a meeting of the Geological Society of London. At the same time the neuroanatomist Grafton Elliot Smith analyzed a cast of the inside of the braincase (which more or less reflects the outside shape of the brain). He found it to be quite "simian." This, he said, was only reasonable given that the human brain had evolved from that of an ape, and he concurred with Smith Woodward that here was the ancestor of modern humans.

Arthur Keith was less enthusiastic. For if, as he thought, the Piltdown fossils were no older than his modern-looking Galley Hill and Ipswich specimens, they could hardly represent an ancestor of modern humans. Moreover, he had considerable reservations about Smith Woodward's reconstruction. Within a few months he had come up with his own, which considerably increased the volume of the cranial vault and even gave the apelike lower jaw a human chin.

This difference was perhaps hardly surprising, since the Piltdown remains certainly left enormous room for conjecture. Most of the forehead and the right side of the skull were missing; and the jaw lacked not only the point at which it had articulated with its cranium, but also the front portion, which would have shown whether or not it had had a chin (modern humans do; apes—and Neanderthals—don't) or a large (apelike) or small (humanlike) canine tooth. Smith Woodward's riposte to Keith's challenge was simple. In 1913 he announced that Teilhard de Chardin had found a lower canine tooth in the gravel pit at Piltdown. And this canine, presumed to be associated with the rest of Piltdown Man, was not only apelike, but remarkably similar to that which he had anticipated in his reconstruction. This appeared to settle the matter in his favor, and by 1915 the consensus in England was that Piltdown, with a small humanlike braincase but an apelike jaw, indeed represented the ancestor of modern humans. Keith, however, maintained his belief that its big brain (as he saw it) notwithstanding, Piltdown, like the Neanderthals, represented a dead end in human evolution. It was not until 1917, when Smith Woodward announced that before his death the previous year Dawson had discovered fragments of a second Piltdown individual at a site some distance away, but on the same stratigraphic level, that Keith yielded to the majority view.

Or, more properly, the English majority view. In continental Europe Boule's early imprimatur was later replaced by the view that the cranium and jaw were unassociated, and continuing resistance came from France in the form of Boule's disciple Henri Vallois's insistence on an alternative form of the "presapiens" theory, the centerpiece of which ultimately became a (still) enigmatic fragment of frontal bone found at the French site of Fontéchevade in 1947. What's more, there had never been much enthusiasm for Piltdown in America. As early as 1915 the Washington mammalogist Gerrit S. Miller had concluded that the Piltdown specimen combined the cranium of a human and the jaw of a chimpanzee. Nonetheless, a new reconstruction of the Piltdown skull undertaken by Elliot Smith in 1922 tipped international opinion (including Boule's) in its favor once more. This reconstruction tended to satisfy all or at least most parties by producing a compromise brain size of some 1,200 ml, about midway between Smith Woodward's and Keith's estimates. And with it the popularity grew of the version of the presapiens theory that held that at some remote point, probably in the Pliocene, a split had occurred in the human lineage. One branch had given rise to the early appearance of modern humans, via Piltdown. The other branch had led to the doomed Neanderthals. Bolstered by the Piltdown fossil, this scheme appeared so persuasive that by the early 1920s almost no paleoanthropologist—not even its author, who had yielded to Boule's influence shortly before his death in 1917—supported Gustav Schwalbe's scheme whereby it was from the Neanderthals that modern humans had stemmed—with the notable exception of one.

The "Neanderthal Phase of Man"

From the outset, the American (formerly Hungarian) physical anthropologist Aleš Hrdlička had viewed the material from Piltdown with the deepest suspicion. Firmly wedded to the view that the human lineage had undergone a steady progressive transformation from an as-yet-undiscovered "anthropoid precursor," and that the modern form had emerged only at the end of the Pleistocene just prior to its spread into the New World, Hrdlička was affronted by Piltdown's combination of apelike and modern human characteristics. Ultimately, while rejecting the claimed antiquity of the cranium, he accepted the jaw as a genuine fossil whose apelike characters were appropriate to its great age and which in turn provided a link with the still earlier fossil ape *Dryopithecus*. His primary concern, however, was to demonstrate the place of the Neanderthals in the direct line of human descent; and in 1927 he culminated a decade and a half of effort in this direction when on a visit to London he addressed the Royal Anthropological Institute with a lecture entitled "The Neanderthal Phase of Man." Defining the Neanderthals as "the Man of the Mousterian Culture," Hrdlička attacked the notion that these hominids had been replaced by invading Aurignacians (the people of the first period of the Upper Paleolithic). Instead, he claimed, the Mousterian had not simply preceded the Upper Paleolithic but had evolved into it. He emphasized the variability in form that existed in the known sample of Neanderthal specimens and suggested that this reflected an ongoing adaptive change in the population—one that was indeed continuing in contemporary human populations in the form of such features as tooth size reduction. "There appears to be," Hrdlička concluded, "less justification in the conception of a Neanderthal *species* than there would be in that of a Neanderthal *phase* of man."

But although Hrdlička was echoing an earlier orthodoxy, and his arguments were to survive to be trotted out again almost verbatim in later years, the immediate impact of his broadside against the "presapiens" idea was almost nil, even when he repeated it at book length in 1930. This was possibly due to the fact that at this point the Piltdown specimens held center stage. Which in turn points to the true significance of these curious remains: more than anything discovered before, they established the importance of the fossil record in documenting humanity's place in nature. Of course, as everyone now knows and some may have done (it's been claimed) as early as 1913, the Piltdown fossils were a hoax. The jaw was indeed an ape jaw, and the cranial fragments, though thick, were those of a modern human. The teeth were filed down, and the bones were stained to look like real fossils before being planted in the pit at Piltdown, along with the (genuine) mammal fossils and the stone tools, for the paleontologists to find. Who the hoaxer was will continue to be debated: almost every possible name has been mentioned, including some pretty improbable ones, although Dawson was clearly involved in some way or another. The only certain thing is that the perpetrator(s) knew the British

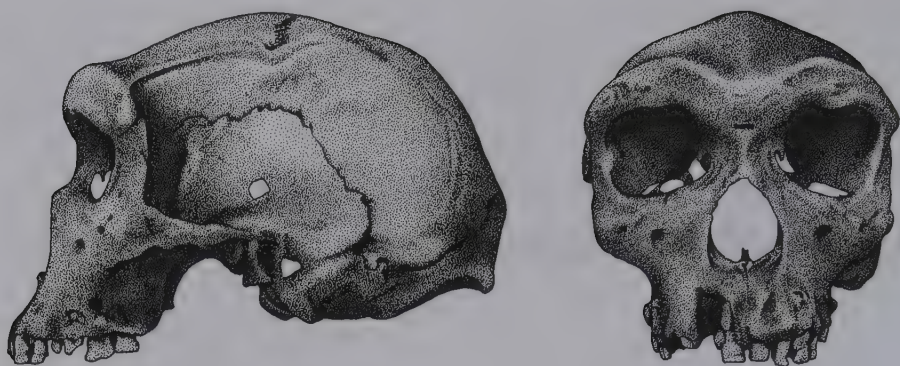
paleoanthropological establishment well enough to know what its members would accept relatively uncritically. And although the anomalous Piltdown Man became increasingly peripheralized as other human fossils accumulated, and was indeed widely ignored by the time its fraudulence was demonstrated in 1953, there is no doubt that for a while it did seriously impede progress in the science of paleoanthropology.

Paradoxically, in its role as "missing link" it was Piltdown that, for the first time, brought the human fossil record squarely into the public eye and established it as a major source of media interest. And it was Piltdown that established the central place of the fossil record in understanding the mysterious process by which modern humans had emerged from an "ape" ancestry. This much is unquestionably on the plus side; but it's also undeniable that paleoanthropology is unique among the subdisciplines of paleontology in ascribing an almost iconic significance to each new fossil that appears. Rarely do paleontologists working on other groups of organisms feel it necessary to undertake wholesale overhauls of their beliefs every time new fossil members of their groups of interest come to light. Paleoanthropologists often do, however, and it's fair to claim that this has been detrimental to their science. Unusual as this paleoanthropological tradition might be, it certainly adds excitement and at least the appearance of progress to the study of human evolution—which may be what we want most out of the study of our own ancestry. And for better or for worse, this way of doing business can be traced back to the Piltdown fiasco.

CHAPTER 5

Out of Africa...

While Piltdown was riding high, and Dubois was once again permitting *Pithecanthropus* to see the light of day, a young Australian anatomist named Raymond Dart traveled from London to take up the Chair of Anatomy at the University of the Witwatersrand (informally known as "Wits") in Johannesburg, South Africa. Shortly before Dart's arrival at Wits in early 1923, a fairly complete fossil cranium of a large-brained extinct human had been found, together with various human and other mammal bones and some stone tools, at the site of Broken Hill (now Kabwe), in Rhodesia (now Zambia). Describing these specimens in late 1921, Arthur Smith Woodward noted resemblances in the face to the Neanderthals and in the skull roof to *Pithecanthropus* (though the brain had been considerably larger than the latter's). Nonetheless, he found the form represented at Broken Hill to be more like modern humans than the Neanderthals were, with a lighter build to its limb bones. To receive this new form Woodward created the species *Homo rhodesiensis*. Further, he remarked that, in the light of Grafton Elliot Smith's suggestion that "refinement of the face was probably the last step in human evolution," this species "may...revive the idea that Neanderthal man is truly an ancestor of *Homo sapiens*; for *Homo rhodesiensis* retains an almost Neanderthal face in association with a more modern brain-case and an up-to-date skeleton. He may prove to be the next grade after Neanderthal in the ascending series." Not a word of comparison with Piltdown! Perhaps this was because, on the evidence of the associated mammalian bones which reportedly all belonged to extant species, he believed the Broken Hill specimen to be comparatively recent: filling of the cave "may not even," he wrote, "have been so remote as the Pleistocene period." Be this as it may, apart from a rather enigmatic and highly incomplete cranium found at the South African site of Boskop in 1913, and an allegedly ancient but modern-looking skeleton recovered at Tanganyika's Olduvai Gorge in the same year, Broken Hill represented the sum total of human fossils known at that time from Africa. As far as human paleontology was concerned, Europe and Asia still monopolized the limelight.



Front and side views of the “Rhodesian Man” cranium discovered in 1921 at Broken Hill (now Kabwe), Zambia. Scales are 1 cm. DM.

Australopithecus

During his time as a junior faculty member at University College London, Dart had worked with Elliot Smith and had absorbed some of his mentor's fascination with the evolution of the human brain. But nothing was further from his mind than the discovery of human fossils when, in 1924, Josephine Salmons, one of his students, brought him a fossilized baboon skull. This had been blasted out of the Buxton lime quarry near a place called Taung, some considerable distance to the northwest of Johannesburg. Dart's colleague R. B. Young, Professor of Geology at Wits, volunteered to bring him more specimens from this site, and into Dart's hands there duly came a fossil consisting of the face and an endocranial cast—a natural mold of the inside of the skull—of an immature hominoid, clearly either an ape or an apelike human. As a neuroanatomist, Dart found his attention first attracted to the brain cast—which in any case, unlike the face, was not enclosed in and obscured by a hard limey matrix. True, Dart's former boss Elliot Smith had studied plaster casts of the insides of various recent and fossil humans and other mammal skulls (“endocranial casts”) and had received a less than ecstatic response. For example, it was objected that the convolutions of the brain itself were often poorly reflected in endocranial casts. Moreover, most of Smith's colleagues held that inferences of the kind that he was willing to make about mental and motor capacities would be hard to justify even where the brain itself was available for external examination. But undeterred by Smith's experience, Dart allowed his appraisal of the brain cast, bolstered by other features of the specimen, to lead him to a far-reaching conclusion. This he arrived at without the usual panoply of scholarship: library facilities were inadequate, he lacked appropriate comparative specimens, and he worked on his specimen alone, in isolation from colleagues.



Front and side views of the "Taung Child" found at South Africa's Buxton Limeworks in 1924. Scales are 1 cm. DM.

Once he had laboriously removed the tough matrix from the face of the "Taung child" (though he had not as yet freed the lower jaw from the upper), Dart immediately prepared a report, which he sent to the London journal *Nature*. This appeared on January 6, 1925, and its title, "*Australopithecus africanus*: The Ape-Man of South Africa," made its message clear. Dart pointed out several features of the face that were obviously humanlike, among them the high, rounded forehead unadorned by eyebrow ridges, the subcircular orbits, the delicate structure of the cheekbones, the flattish profile, and the lightly built lower jaw. He also considered the teeth (which corresponded to those of a modern six-year-old, with just the first permanent molar in place) to be "humanoid." The milk canines barely projected beyond the other teeth, the incisors were small, there was no diastema (the gap between the canine and front premolar in the ape lower jaw that receives the large upper canine when the mouth is closed), and so forth. Most of these characters were actually related more than anything else to the tender age of the individual, for in both apes and humans the juvenile face is small relative to the braincase, and delicately built. The brain cast preserved the entire right side of the brain, with minor damage here and there. It was small (modern estimates put the volume of the whole thing at 440 ml), and Dart confessed that in the adult it would probably not have surpassed a gorilla's in size. Nonetheless, he saw in it evidence for a greater expansion than in the apes of the higher centers of the brain, with a "rounded and well-filled-out contour, which points to a symmetrical and balanced development of the faculties of associative memory and intelligent activity." Most significant, Dart thought, was the humanlike backward displacement of the lunette sulcus, a groove which marks the front of the brain's primary visual cortex. What any such displacement would reflect

was an increase in the extent of the "association" cortex that lies in front of the sulcus, and this suggested to Dart that his creature had "laid down the foundations of that discriminative knowledge of the appearance, feeling and sounds of things that was a necessary milestone in the acquisition of articulate speech." It had also, he believed, acquired the habit of upright walking, since the inferred position of the foramen magnum, through which the spinal cord exits the brain, was right underneath the skull, rather than toward the rear as in the quadrupedal apes.

In 1925, ways of assessing relationships between organisms were rather rudimentary, based primarily on overall resemblance—which generally summed out as the intuition of the observer. It was not yet realized (and was not to be for many decades yet) that terms such as "ape-like" and "human-like" were by themselves essentially meaningless when it came to assessing taxonomic relationships. Dart cannot be faulted for analyzing his fossil in these terms; but reading between the lines of his description suggests that his basic attitude toward the specimen was founded in a tradition that was archaic even in his day. "The whole cranium," he wrote, "manifests in a striking degree the *harmonious relation* of calvaria [braincase] to face emphasised by Pruner-Bey." His reaction harks back to the essentialist aesthetic that had informed reaction to the earliest human fossils to come to light. This had emphasized the "brutishness" of the apes and even of the "lower races" of humans, in contrast to the civilized elegance of the "higher races;" and indeed the French savant Franz Pruner Bey, to whom Dart referred, has gone down in history as the man who wrote off the Feldhofer Neanderthal as a strongly built Celt, "somewhat resembling the skull of a modern Irishman with low mental organization." It may be of significance in this regard that Dart himself was no fan of *Pithecanthropus*, which he described as "a caricature of precocious hominid failure."

But although it was the "humanoid" aspects of his specimen that most impressed Dart, the name he chose for its species, *Australopithecus africanus*, translates as "southern ape of Africa." Indeed, he described it himself as a "man-like ape," a representative of "an extinct race of apes *intermediate between living anthropoids* [apes] *and man*." This "race," while "well advanced beyond modern anthropoids in just those characters, facial and cerebral, which are to be anticipated in an extinct link between man and his simian ancestor," had at the same time a small sized brain "lacking the distinctive, local expansions which appear to be concomitant with and necessary to articulate man." It was thus "no true man," and Dart proposed a new family, Homo-simidae, to contain it. Noting that the site of Taung was right on the edge of the Kalahari Desert, and believing that the harsh climate of the area had been stable back into the remote past, Dart proposed that "[f]or the production of man a different apprenticeship [from that served by the apes in the "luxuriant forests of the tropical belts"] was needed to sharpen the wits and quicken the higher manifestations of intellect—a more open veldt country where competition

was keener between swiftness and stealth, and where adroitness of thinking and movement played a preponderating role in the preservation of the species." I love this last passage, though Dart was to be roundly condemned by his colleagues for excessive rhetoric. For, as he reveals himself here, Dart was the first student of the human fossil record who seems to have felt viscerally the drama of the biological history of mankind. He was certainly among the first to perceive that the story of our species is one of individuals, populations, and species living, striving, and dying as part of an enormously complex web of organic life, and to see that this story is not complete if we do not let ourselves go well beyond the teeth and bones that are our primary evidence of it. Dart was to allow his vivid imagination get the better of him on later occasions, but here I cannot help but feel that, even though he was writing in the august pages of *Nature*, he had hit a needed note.

Few at the time agreed. In England, either you are "sound" or you are not. And according to the distinguished anatomist W. E. Le Gros Clark, Dart's soundness had been in question ever since, before leaving University College, he had co-authored a paper which gave the impression that he "might be inclined too hastily to arrive at conclusions on too little evidence." And many felt, on reading his *Nature* article, that his purplish prose might hint once more at overenthusiastic conclusions. The week following the publication of his article, four of the greats of British palaeoanthropology delivered their judgments in *Nature*. These were based, of course, entirely on Dart's description and illustrations, for none of these scholars had seen the original specimen or even a cast (replica) of it. Casts, in fact, were slow to follow (nobody in Dart's department knew how to make them, and eventually a professional plasterer was hired for the job!) and first reached England not for the delectation of Dart's colleagues, but for display to the public at the British Empire Exhibition that opened in the summer of 1925. The British paleoanthropological establishment, forced to peer at the specimen through glass while being jostled by the passing hoi polloi, was not amused.

But given the circumstances, the generally unfavorable reaction among Dart's colleagues was understandable. It is always hard to know what to make of a fossil when only photographs and someone else's description are available. Many of the "humanoid" features to which Dart had pointed might as well have been attributed to the tender age of his specimen; the features of the brain cast are still being argued over to this day, and Dart had given not one hint as to the geological age of his fossil—though it was clearly old, whatever that might mean. So most initial reactions were perhaps justifiably cautious. Arthur Keith inclined toward placing *Australopithecus* in the same subfamily as the African apes. Elliot Smith was intrigued but reserved his opinion, particularly pending the opportunity to evaluate the teeth once the lower jaw was detached from the upper face. Smith Woodward, champion as ever of Piltdown, dismissed Dart's specimen out of hand, claiming that it "certainly has little bearing on the question" of whether humans evolved in

Asia or Africa. Finally, the Cambridge anatomist W. L. H. Duckworth, upon whose treatise *Morphology and Anthropology* Dart had relied heavily in comparing the Taung infant to the apes, admitted certain "advanced" features of the skull but found its closest resemblance to be with the gorilla. Overall this response was pretty tepid, but it was certainly preferable to the public reaction to newspaper coverage of Dart's claims. One correspondent accused Dart of being a Priest of Baal; someone wrote from France to inform him that he would "roast in the quenchless fires of Hell;" an Englishman hoped to see him in "an institution for the feebleminded."

For some reason (probably because at heart he was interested in brains, not bones; he had, after all, only stumbled into paleoanthropology by accident), Dart did not seek at the time to bolster his case by looking for adult *Australopithecus* fossils at Taung or at any of the other lime mines that dotted the landscape of central southern Africa. And although his University almost immediately offered him the opportunity to travel to show his prize to his colleagues and to compare it directly with specimens in the great natural history institutions of Europe, it was not until 1931, by which time attitudes had generally hardened, that he brought the Taung juvenile to England where it could be examined at first hand by his colleagues. And by then, moreover, paleoanthropological attention had been attracted away from Africa and toward Asia once more.

Peking Man

For some time paleontologists had suspected that climatic change might have been the factor that initiated the divergence of the human lineage from that of the apes. And in certain influential quarters it was believed that the most likely locus of such change was central Asia, where uplift of the Himalayas had combined with a general post-Eocene trend toward climatic cooling and drying to create open high plains. Any ape living in this part of the world would have had to abandon a forest-living existence in favor of one in a more open-country habitat, perhaps with the consequences hinted at by Dart in his discussion of *Australopithecus*. The principal proponent of this viewpoint was Henry Fairfield Osborn, President of the American Museum of Natural History. This distinguished paleontologist was so convinced that Central Asia would prove to be the cradle of mankind that during the 1920s the American Museum sponsored a remarkable series of expeditions to the region. There, Osborn believed, "while the anthropoid apes were luxuriating in the forested lowlands of Asia and Europe, the Dawn Men [had been] evolving in the invigorating atmosphere of the relatively dry uplands." In the event, while the expeditions made many extraordinary discoveries, they failed to find any human fossils. Still, they did have the effect of drawing public and paleoanthropological attention to this part of the world. The fact that Osborn was at the same time tending more and more to reject an ape ancestry for humans, or at



Side view of the most complete of the "Peking Man" crania (Skull XII) discovered in the prewar period at Choukoutien (now Zhoukoudian), China. Scale is 1 cm. DS.

least to push it as far back into the remote past as possible, detracted not at all from the attractiveness of the Central Asian scenario.

But as it happened, by the time the American Museum expeditions got underway, paleontological work had already been started in China. This was principally as a result of the zeal of Johan Gunnar Andersson, a mining engineer by trade but a paleontologist by avocation. Through his efforts, a monopoly on fossil seeking in that country had already been obtained by scientists affiliated with the University of Uppsala, Sweden. Thus excluded by official agreement from working in China, the Americans confined their attention to the uplands of Mongolia, where the rocks were so ancient that nobody without Osborn's peculiar viewpoint on the matter would have expected to find the remains of early humans—though much else of great interest was found. The Europeans, on the other hand, directed their attention among other things toward more recent cave deposits, from which "dragon bones," otherwise fossil mammal teeth, had long been known. In this they received valuable advice from the distinguished paleontologist Walter Granger, an advance man for the American Museum team. One of the sites they explored, an abandoned lime mine not far from Beijing, was Chou K'ou Tien (now Zhoukoudian).

This work was not long in yielding results. The fill from the Zhoukoudian cave was rich in fossils, and by the summer of 1921 it had already yielded the first direct evidence (Andersson had already identified correctly the rather crude stone tools that were abundant at the site) of what was to become known as Peking Man. But for his own reasons, its discoverer, a young Austrian paleontologist named Otto Zdansky, kept its discovery secret until 1926. In that year, at a meeting held in Beijing, he described two human teeth from the fossil assemblage at Zhoukoudian. Zdansky himself declined to make much of this find, but Davidson Black, a Canadian who was then Professor of Anatomy at the Peiping Union Medical College, was fired with enthusiasm. He arranged financing from the Rockefeller Foundation, sponsors of the Medical College, and new excavations began at Zhoukoudian in the spring of 1927 under the

field direction of a young Swede named Birger Bohlin. By the fall of that year, another human tooth had been recovered. Black had regarded the two original teeth as belonging to the genus *Homo*, but on the basis of this new discovery he created the new genus and species *Sinanthropus pekinensis*, the "Chinese man of Peking." Few were impressed. One tooth, which was all Black had to show his colleagues when he visited Europe (the original two teeth were in Sweden), was not much on which to base an entire new genus of humans. But Black persevered, and with continuing Rockefeller support he established the Cenozoic Research Laboratory in Beijing, the first project of which would be to enlarge the excavations at Zhoukoudian, employing a largely Chinese team.

Enormous quantities of the cave deposit were removed and processed, and thousands of mammalian fossils were recovered, among them a few more human teeth. But it was not until the end of 1929 that these labors paid off with the recovery of a braincase of *Sinanthropus*. This was the beginning of a stream of new discoveries that continued beyond Black's early death in 1934, until guerilla activity around Zhoukoudian brought work there to a halt in 1937. By that point, the site had yielded 14 partial skulls as well as various bones of the postcranial skeleton of *Sinanthropus*. All of this engaged the interest of an eager public—whose attention was thereby distracted from *Australopithecus*—but, from the moment that the Chinese paleontologist W. C. Pei had recovered the first braincase in 1929, it was clear that here was an early human very much like the one from Java. The forehead of the first Zhoukoudian braincase—like later ones—was a little steeper than in Dubois's *Pithecanthropus* from Trinil, and the brain capacity a little larger; but Black was more impressed by the similarities than by the differences between this pair of early humans. Still, he continued to use the name *Sinanthropus*, implying that the two fossils indeed belonged to different genera. For Black, *Sinanthropus* was simply a more advanced form, occupying a position intermediate between *Pithecanthropus* and the Neanderthals.

Predictably, Eugene Dubois disagreed with all this, if in an odd way: *Sinanthropus*, he thought, was "perfectly" human—probably, indeed, a Neanderthal, though he later retracted this idea—while *Pithecanthropus* showed some apelike characteristics, especially in the brain. To maintain the integrity of his theory of brain evolution, Dubois was concerned above all to show that *Pithecanthropus* did not occupy the same level of evolutionary development as either humans or living apes, and the advanced features to which the describers of *Sinanthropus* pointed thus forced him to distance the Peking finds from his own fossil. To the world, however, *Sinanthropus* convincingly demonstrated that *Pithecanthropus* was indeed an early human, and as material from Zhoukoudian accumulated, most authorities soon came to believe that both represented the same group of early humans. Particularly influential in this regard was the fact that by the end of 1934 a series of skullcaps had been found at Zhoukoudian in which brain size varied from 850 to 1,200 ml, a range within which the Trinil skullcap comfortably fitted.

One thing that set off the Zhoukoudian finds from those in Java was a fuller reported archaeological context. In 1931, Black stated that some of the animal bones from Zhoukoudian had apparently been charred by fire, and that tests had shown some blackened layers of the cave deposits to contain quantities of carbon. No actual hearths were found, as had been in some of the later European cave sites, but his evidence was enough to convince Black that *Sinanthropus* had included the control and use of fire among its behaviors. In the same year W. C. Pei had reported finding crude quartz and other stone artifacts at Zhoukoudian, so Peking Man was rapidly acquiring many of the behavioral traits generally associated with humans. By 1939, moreover, Black's successor, the German anatomist Franz Weidenreich, had added the less attractive traits of murder and cannibalism to the relatively anodyne pursuits of tool and fire use. Weidenreich noted that the remains of almost 40 human individuals, 15 of them children, had been found in the cave, but that there was not one complete skeleton. Indeed, the fossil human remains were overwhelmingly cranial, and all were fragmentary, many bearing apparent evidence of physical trauma while still covered in soft tissues—apparent witness to their bearers having “suffered violent attacks.” All of the Zhoukoudian bones, human and nonhuman alike, were thought by Weidenreich to be the remains of *Sinanthropus*’ meals. Further, the bases of all the human crania were broken, presumably for cannibalistic removal of the brain within. This is an explanation evoked on numerous occasions before and since to explain damage to the bases of fossil human skulls, and Weidenreich was particularly impressed by the claims of the anthropologist Paul Wernert that, from prehistoric times to the present, “there had always existed an entanglement between the two rites of anthropophagy and head-hunting,” based on the notion of “increasing the material and spiritual qualities of an individual or the community taking possession of the corpse of the vanquished.” Taking all these indications together, Weidenreich could not avoid the conclusion that “the *Sinanthropus* population of Choukoutien had been slain and that subsequently their heads were severed from the trunk, the brain removed and the limbs dissected.”

While realizing that “it may prove rather distressing to some sensible people to hear that the most primitive ancestor of recent mankind had been responsible for such terrible acts as manslaughter of women and children and cannibalism,” Weidenreich also regretted that his audience would not find the behavior of other fossil humans “any more pleasing.” “Ten years ago,” he wrote,

I was already able to show that the fossil man of Weimar-Ehringsdorf, a representative of the Neanderthal group of the last interglacial period, must have indulged in similar customs. The skull was broken like those of *Sinanthropus*, the frontal bone shows very characteristic markings of heavy blows, and the base is missing... The remains of the Krapina population, who lived during the same period as the man of Weimar-Ehringsdorf, were

so completely broken that it was even impossible to reconstruct one entire brain case from the numerous bone fragments belonging to some 20 individuals....The recently discovered skull of Steinheim, who may be even older than the Weimar-Ehringsdorf and Krapina man, also shows...manipulations similar to those shown in *Sinanthropus* skulls.

Some disagreed, as would many today, if not necessarily for the same reasons. Marcellin Boule, for example, felt that *Sinanthropus* was entirely too primitive to have made the stone tools, or to have lit the fires, or to have hunted the animals of Zhoukoudian. In his view another more advanced human must have lived there and been responsible for the ashes and tools, and for the accumulation within the cave of the bones of *Sinanthropus* and other animals. He did not find it surprising that there was no trace of this advanced human in the fossil record of Zhoukoudian, for, as he pointed out, there were plenty of other fossil sites with evidence of human occupation, but no human bones. Nonetheless, Weidenreich's interpretation generally prevailed—and, as it happened, foreshadowed a more comprehensive scenario of a bloodstained human past that was shortly to emerge from Africa.

Back to Java

As work continued in China, attention was once again being paid to the fossil potential of Java. In 1931 and 1932 the Dutch mining engineer W. F. F. Oppenoorth recovered a series of 11 crania, varying in brain capacity from 1,035 to 1,255 ml, from a site (now known as Ngandong) in the Solo Valley of western Java. These fossils were reckoned to be of late Pleistocene age, thus younger than the early Pleistocene date the Zhoukoudian fauna seemed to suggest for the Peking Man specimens. However, they resembled the latter in certain ways, although Oppenoorth was initially more impressed by their similarities to the Neanderthals. And while Oppenoorth later preferred to emphasize the differences between the Solo skulls and those of the Neanderthals, many came to see *Javanthropus* (or *Homo soloensis*) as a sort of Asian Neanderthal equivalent.

Discoveries in Java that received considerably more attention were made by the German paleoanthropologist Ralph von Koenigswald in 1936 and the years following. The first human fossil that von Koenigswald recovered, at a place called Modjokerto, was the cranium of a child that he believed to be of early Pleistocene age. He clearly thought this young specimen to be a *Pithecanthropus*, but in deference to the opposition of Dubois, who likened it to the Solo skulls, which he believed to be ancestral to the aborigines of Australia, von Koenigswald named his new find *Homo modjokertensis*. He did not, however, extend the nomenclatural courtesy to a very robust jaw fragment he found close to the village of Sangiran. This he squarely placed in

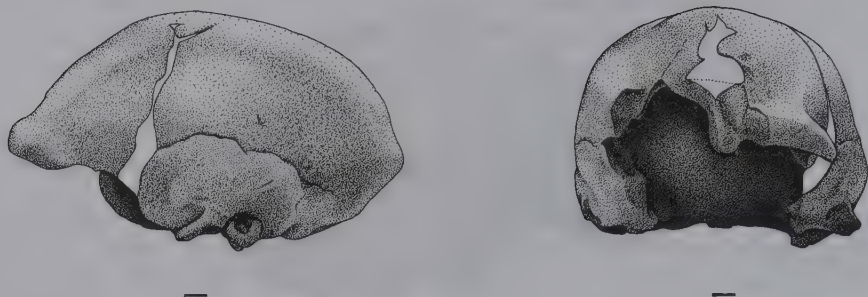


Side view of one of several crania (Skull V) discovered at Ngandong (Solo), Java, during the 1930s. Scale is 1 cm. DS.

Pithecanthropus, with which he considered it coeval. By 1937 von Koenigswald had obtained a skullcap from nearby sediments at Sangiran. The specimen was more complete than Dubois's Trinil fossil, but in comparable features the two were pretty alike, and proved beyond a doubt that *Pithecanthropus*, like *Sinanthropus*, lay in the human family. von Koenigswald estimated its cranial capacity at about 750 ml; more recent estimates make it a little larger than this, but still smaller than the Trinil specimen. Partly because of the smallish brain size, von Koenigswald considered his *Pithecanthropus* to be more primitive than *Sinanthropus*. These initial finds were followed over the next several years by others, including the back part of another skullcap with an associated maxilla and a massive mandible. Various names were assigned to this material, but differences in size and robustness between different specimens were eventually ascribed to sexual dimorphism—size and shape differences between males and females.

Unfortunately, geological controls on the excavation of all of the Java fossil collections were extremely poor. Hence the exact dating of the Trinil, Sangiran, and Solo specimens remains debated today, though a time span that includes almost the whole of the Pleistocene probably elapsed between the oldest materials from Sangiran and the latest from Solo.

In 1939 von Koenigswald journeyed to China to compare his fossils with the *Sinanthropus* materials, by then under the care of Franz Weidenreich. Following the cessation of excavations at Zhoukoudian, Weidenreich had devoted himself to intensive anatomical study of the by then numerous *Sinanthropus* specimens and had already begun to form an explicit theory of human descent in which the various human races could be traced far back in the fossil record. He had done this partly to provide an alternative to the old polygenist view of human origins, which he dismissed out of hand (though he saw plenty of evidence in the fossil record for a "polycentric" origin of modern mankind). Each race, Weidenreich thought, had evolved separately toward



Front and side views of the braincase ("Pithecanthropus II") discovered at Sangiran, Java, in 1937. Scales are 1 cm. DM.

Homo sapiens, following some form of inner directionality linked to enlargement of the brain. And even at a time when developments in evolutionary theory were making such ideas distinctly outmoded, Weidenreich was not reluctant to attribute this directionality to orthogenesis, the notion that evolution is somehow goal-oriented. In this broader scheme Weidenreich placed *Sinanthropus* as a precursor specifically of the "Mongol" (Asiatic) race.

To Dubois's dismay, before von Koenigswald's arrival in Beijing Weidenreich had already found points of distinction between the partial femora from Zhoukoudian and the femur from Trinil. These had persuaded him that the Trinil skullcap and femur were not associated with each other, though he accepted a general affinity between the species represented by the skullcap and that from Zhoukoudian. On the other hand, he was initially impressed by the resemblances between the Sangiran material and the Solo skulls. He suggested that at Sangiran von Koenigswald might have found female members of the species represented at Solo, and he contested the view that *Pithecanthropus* was more primitive than *Sinanthropus*. Direct comparison of the Chinese and Javanese specimens, however, persuaded both Weidenreich and von Koenigswald beyond a doubt that these "prehominids" were "related to each other in the same way as two different races of present mankind, which may also display certain variations in the degree of their advancement." As to which was the more "advanced," they wisely refused to be categorical, though they did agree that "Pithecanthropus shows some significant characteristics which must be considered more primitive than those evident in *Sinanthropus*."

Interestingly, while they continued to use the terms "*Sinanthropus*" and "*Pithecanthropus*" in their joint report to *Nature*, von Koenigswald and Weidenreich did not italicize them. This is obligatory for formal zoological names, and both authors had adhered to this convention when referring to the respective forms in earlier publications. Moreover, in their joint paper they italicized *Homo soloensis*, which they considered to be the next step in human evolution. This suggests that they were using these genus names (as I shall from now on) simply for the sake of convenience, and that if pressed



Map showing the locations of the major sites of human fossil discovery in eastern and southeastern Asia. S,T,N denotes the approximate location of Sangiran, Trinil, and Ngandong. Sambungmacan and Ngawi are also in this area. DS.

they would have allocated Java and Peking Man to *Homo* as well. Certainly Weidenreich went on to develop his theory of a Sinanthropus–Mongol connection to state specifically that “at the very appearance of true hominids [represented by Pithecanthropus and Sinanthropus] there must have existed several branches, morphologically well distinguishable from one another, which all proceeded in the same general direction with mankind today as their goal.” Pithecanthropus, he believed, was on the line, via *Homo soloensis* and “Cohuna Man” (a relatively recent fossil Australian), to modern aboriginal Australians; modern Chinese are derived from Sinanthropus via intermediates as yet unknown; later African ancestry was represented by the “Neanderthaloid” Rhodesian Man; and while Neanderthals appeared to have been replaced in western Europe by invading moderns, it was not out of the question that they had evolved elsewhere into the form which subsequently supplanted them. In its essentials this scheme has shown remarkable tenacity in surviving right up to the present day, albeit in a somewhat modified form.

Sadly, the Peking Man fossils did not long see the light of day. Davidson Black had established the Cenozoic Research Laboratory on the understanding that the Zhoukoudian fossils would remain in China, but fears grew for the safety of the specimens as the Japanese encroached on China throughout the period leading up to the outbreak of war in the Pacific. These fears were not unfounded: despite precautions taken by von Koenigswald before

his internment following the Japanese takeover of Java, one of the Solo skulls wound up in the Japanese Imperial Palace in Tokyo. As the situation in China deteriorated, the possibility was broached of sending the human fossils from Zhoukoudian to a place of temporary refuge in the United States. During most of 1941 the custodians of the fossils dithered over how and when this should be done, and Weidenreich did not take them with him when he left at midyear to take up residence at the American Museum of Natural History. In the event, the crucial decision to export them was not taken until just before the outbreak of formal hostilities between Japan and the United States in December 1941. When, on December 8, the Japanese searched the fossils' repository they found only casts; what had happened to the original fossils remains a mystery. The specimens appear to have been packed in a couple of footlockers and entrusted to a platoon of U.S. Marines for transportation to the port of Tientsin. There they were to be loaded on the S.S. *President Harrison*, bound for the United States, but the ship was sunk en route to the port, and the fossils simply vanished. To this day the fate of the Zhoukoudian bones remains unknown, though theories abound. Fortunately, though, before his death in 1948 Weidenreich was able to complete a series of exquisitely detailed monographs on *Sinanthropus*, and what for their period are technically excellent casts still remain to represent the originals, pale substitute though they are. Postwar excavations at Zhoukoudian have produced a few more human fossils, including another braincase, but nothing like the prewar riches.

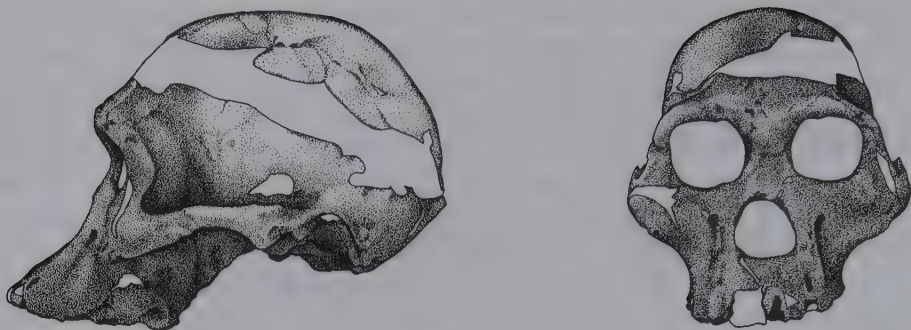
Still, whatever the fate of the Peking Man fossils, together with von Koenigswald's specimens they had served the critical purpose of validating Dubois's original finds. It is hard for us to appreciate it today, but as late as 1938 an anonymous commentator was able to write in *Nature* that "of recent years, opinion has tended in an increasing degree to incline" to the view that Dubois's *Pithecanthropus* remains were ape rather than human. By the time that *Sinanthropus* disappeared, that had irreversibly changed. No question, then, that the finds from eastern Asia deserved the limelight in which they basked during the 1930s; but in Africa, with less fanfare, equally significant developments were meanwhile afoot.

CHAPTER 6

...Always Something New

One of the most remarkable characters in the history of paleoanthropology was Robert Broom. A Scot by birth, a physician by training, and initially with a consuming interest in the origin of the mammals, Broom traveled in 1892 to Australia, home of the world's most primitive mammals. After five years he moved on to South Africa, which was to be his home for the remainder of his long life. After describing a fauna of small mammals from a Pleistocene bone breccia, Broom shifted his interest to the fossil-rich sediments of the Karroo region of central South Africa. He rapidly became the leading world authority on the mammal-like reptiles that these rocks produced in extraordinary abundance. An early (and for many years the only) wholehearted supporter of Dart's interpretation of *Australopithecus* as an ape-human intermediate, Broom gave up the practice of medicine in 1934 at the age of 68 and took up a post at Pretoria's Transvaal Museum. He busied himself with reptilian fossils for his first couple of years at the Museum; but in 1936, by which time no effort had been made in 12 years to recover adult *Australopithecus* specimens, Broom resolved to rectify this situation. Short of funds, he looked for cave deposits closer to home than Taung—not a difficult thing to do, since solution cavities were hardly lacking in the soluble dolomitic limestones of the Transvaal. Most of these were filled with accumulated rubble cemented together by redeposited lime, and many were the sites of limeworks. Broom's attention was rapidly drawn (by Trevor R. Jones, a student of Dart's) to a lime mining operation at Sterkfontein, only about forty miles from his office in Pretoria. Coincidentally, the manager there was the same man who had been in charge at Taung when Dart's juvenile *Australopithecus* had turned up. In August of 1936 the site yielded a rather battered and incomplete adult *Australopithecus* skull, which Broom immediately reported to *Nature* as confirming Dart's views.

The associated fauna suggested to Broom that the Sterkfontein deposit was somewhat younger than the one at Taung, so he placed his find in a new species, *Australopithecus transvaalensis*. Later, impressed by differences that he perceived between the teeth of the Taung and Sterkfontein specimens



Side and front views of the cranium Sts 5 ("Mrs Ples") from Sterkfontein Member 4, South Africa. This is the best known of the crania attributed to *Australopithecus africanus*. Scales are 1 cm. DM.

(though his fossil had only four teeth and the Taung child had erupted only the first permanent molars), he shifted his specimen into a new genus, as *Plesianthropus* ("near man") *transvaalensis*.

There was no doubt in Broom's mind that he had before him the confirmation of Dart's claims that he had been seeking. Among his European colleagues, however, news of his finds was received politely but without enthusiasm. Arthur Keith's dismissal of *Australopithecus* in his *New Discoveries Relating to the Antiquity of Man* of 1930 (which had preempted a long monograph prepared by Dart) was regarded in Britain as the last word on this creature, and the conclusion by the German Wolfgang Abel that the Taung baby was but a juvenile ape was similarly influential on the Continent. In this intellectual climate Broom's fragmentary fossil was regarded as hardly sufficient evidence to justify abandoning the conventional wisdom that *Australopithecus* was no more than an early ape. Broom persevered, however, and over the several months following his initial discovery he recovered a few more bits and pieces from Sterkfontein. But his next real break came in June 1938, when a local schoolboy, Gert Terblanche, found a palate with a partial dentition at a neighboring site called Kromdraai, just across the valley from Sterkfontein. Other finds there followed, and pretty soon Broom had assembled half a skull of a form more heavily built than his *Plesianthropus*, with a flatter face and much larger chewing teeth. These differences led Broom to create yet another genus and species, *Paranthropus* ("next to man") *robustus*, and as he worked on the block of matrix from which the first specimens had been removed, he found a few bones of the postcranial (body) skeleton, including a very humanlike talus (ankle bone).

International Acceptance

In America, Broom's views on the proto-human status of *Australopithecus* rapidly gathered support from the influential paleontologist and comparative



Slightly distorted lower jaw (TM Sts 53B) attributed to *Australopithecus africanus*, with complete but somewhat damaged dentition, from Sterkfontein Member 4, South Africa. Scale is 1 cm. DM.

anatomist William K. Gregory of the American Museum of Natural History. With his colleague Milo Hellman, Gregory traveled to South Africa in June 1938 to view the original specimens from Taung and Sterkfontein, just as the first fossils from Kromdraai were coming to light. Gregory and Hellman's appraisal of the dental evidence, in particular, led them to the conclusion that here were "in both a structural and a genetic sense the conservative cousins of the contemporary human branch." "The whole world," Gregory told a meeting of the Associated Scientific and Technical Societies of South Africa on July 20, 1938, "is indebted to these two men [Broom and Dart] for their discoveries, which have reached the climax of more than a century of research on that great problem, the origin and the physical structure of man." To Gregory and Hellman the South African fossils were true intermediates between extinct Miocene apes such as *Dryopithecus* and modern humans. In 1939, while reserving judgment on whether *Australopithecus*, *Plesianthropus*, and *Paranthropus* actually deserved to be recognized as separate genera, the American scientists formally placed them all in the same subfamily, Australopithecinae, of the family Hominidae. The other hominid subfamily, Homininae, contained modern humans and their postaustralopithecine precursors. The apes, in contrast, occupied their own family, Pongidae (for *Pongo*, the orangutan).

Another early supporter of the human affinities of the australopithecines was Ralph von Koenigswald, who declared in 1942 that he could find in the dentition "no characteristic to force this group from the Hominidae."

Nonetheless, he could not consider them ancestral to humans, partly because he believed they were geologically too young, but also because their teeth were too large. Recognizing that this latter factor was no obvious impediment to ancestral status, von Koenigswald felt obliged to elaborate. First, he said, it was a general law that organisms became larger over their evolutionary histories, as exemplified by the increase in size over time of the human brain. But *Pithecanthropus*, *Sinanthropus*, the Neanderthals, and modern people formed a series in which tooth size decreased, and this required special explanation. His explanation lay in the use of tools to prepare food and in the use of fire to cook it—and for this there appeared to be abundant evidence from Zhoukoudian onwards. With these innovations, mankind “used his teeth in a different way from his anthropomorphic ancestors. When he began to talk he also used his jaw muscles in a different way. Only in the development of civilization can we find a reason for the typically human evolution: the reduction of the dentition combined with an astonishing, progressive development of the brain—the two surely interdependent.” So far so good—perhaps. But von Koenigswald went on to suggest that because tooth size increase was inevitable in the absence of civilizing factors, *Pithecanthropus*, probably the first human to bear civilization in his sense, must have had the largest teeth ever possessed by a member of the human lineage. From this it followed that “every human-like being having bigger teeth than *Pithecanthropus* must be excluded from the direct line of human evolution.” The australopithecines, regrettably, fell into this latter category. By the middle of the twentieth century, reasoning of this kind would have attracted incredulity in any other branch of paleontology, but it is a testament to the continuing insularity of paleoanthropology that to von Koenigswald’s colleagues it did not sound unduly out of place.

Doubtless fortified by the support of Gregory and Hellman—though in any event it was not in his character to be assailed by self-doubts—Broom labored throughout the years of the Second World War on a monographic treatment of his finds. In this work, which appeared in early 1946 when he was almost eighty, Broom concluded that his australopithecines had walked bipedally and reiterated his and Gregory’s conclusion that although they had relatively large faces, their dentitions were of human type (teeth are particularly important to paleontologists because, as the hardest tissues of the body, they are more frequently preserved as fossils than other structures). They had small brains, “probably between 460 cc [1 cc = 1 ml] and 650 cc” (the former turns out to be about an average figure, the latter something of an overestimate), but they probably had advanced manipulative abilities that embraced tool use. Altogether, wrote Broom of the australopithecines, “if one could be found alive today I think it probable that most scientists would regard him as a primitive form of man.” He noted the geological evidence that suggested these creatures had lived in open country; and as to geological age, on faunal grounds Sterkfontein appeared to date from the middle or late Pliocene, Taung possibly from a bit earlier, and Kromdraai from somewhat later, possibly the

early Pleistocene. Later humans, Broom believed, were derived from a Pliocene australopithecine not very different from *Australopithecus*.

Impressive though Broom's monograph was, however, it was received by his British colleagues with a notable lack of enthusiasm. According to Wilfrid Le Gros Clark this was partly because it bore certain marks of haste in preparation, but principally because it was published along with what was considered to be an overambitious appraisal of the available brain casts, natural and artificial, from all three sites. This had been prepared by G. W. H. Schepers, a colleague and former student of Dart's who claimed to be able to deduce a whole range of humanlike behaviors from the bumps and grooves on the casts. What's more, Schepers vigorously attacked the idea that humans could be descended from "specialized and degenerate anthropoids;" and under the influence of the anatomist Frederic Wood Jones (who had developed his own theory of human descent not from the apes, which he considered an altogether separate lineage, but from an Eocene form resembling the tarsier, a small and enigmatic primate), he argued that the human lineage had been distinct since the Eocene. Schepers' arguments did not go down well, and Broom's simpler if not entirely restrained reasoning was tainted by association. Indeed, it was not until 1947, when Clark himself visited South Africa and examined the full range of australopithecine material that the tide began to turn. Clark was the first member of the British anthropological establishment to have studied all these fossils at first hand and, sceptic though he initially was, he rapidly became convinced that Broom was right. When he took his new message back to England, he ran into some opposition from Wood Jones and his fellow anatomist Solly Zuckerman, an instinctive and intransigent reactionary; but his authority rapidly carried the day.

Even Broom's exact contemporary Arthur Keith recanted, writing in 1948 in his *A New Theory of Human Evolution* that "of all the fossil forms known to us, the australopithecinae are the nearest akin to man and the most likely to stand in the direct line of man's ascent." But although he accepted that these forms showed that a large brain must have been acquired in the course of the evolution of the human lineage rather than having been present at the outset, Keith found himself unable to regard them as early humans. This was because to him, as to many others, small brains were by definition apelike, and the presence of small brains in early members of the human lineage made it necessary to define a "cerebral Rubicon" in brain size: a threshold which had to be exceeded by anything with a claim to being human. This threshold he set at 750 ml, and he noted that though the test was passed by *Pithecanthropus*, the australopithecines failed it. Piltdown, of course, passed as well, but, though its fraudulent nature had not yet been demonstrated, Piltdown had by this point become something of an embarrassment and Keith was forced to shunt it into an evolutionary siding, as an "aberrant" form which had later become extinct. Interestingly, at about the same time in America the Harvard anthropologist E. A. Hooton was wrestling with the same problem and reached a more

negative conclusion about the australopithecines because they "lacked the brain overgrowth that is specifically human and perhaps should be the ultimate criterion of a direct ancestral relationship to man of a Pliocene precursor. Because they lacked brains they remained apes, in spite of their humanoid teeth. Since the Australopithecinae died out in Africa, while the gorilla and chimpanzee survived, it would appear that a thorough-going ape is better than half a man." The logical flaw (or series of them) is glaring indeed, but perhaps it is redeemed by Hooton's poetic contribution to the argument over the australopithecines:

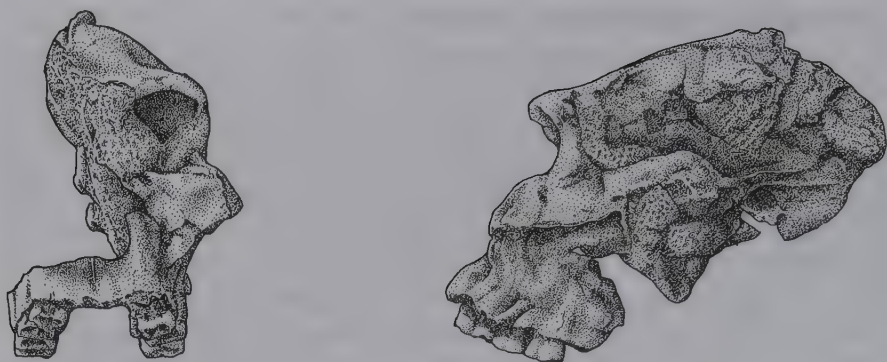
Cried an angry she-ape from Transvaal
 Though old Doctor Broom had the gall
 To christen me Plesi-
 anthropus, it's easy
 To see I'm not human at all.

No energy need have been wasted on this empty argument if the various protagonists had taken a moment to consider how great a stumbling block the vagueness of the concept of "human" (and of "ape," come to that) is to the understanding of our evolutionary history. Until the idea of evolution arrived on the scene it was, of course, obvious what "human" and "ape" meant: living *Homo sapiens* with all of its unique attributes on the one hand, and the chimpanzee and its like on the other. But with the idea of evolution came the notion of intermediates: that we are joined to the rest of the living world. And in this view the question with which Keith and others struggled seemed inevitably to arise: At what point did our precursors, less and less like ourselves as time recedes, become human? (We less often ponder the other side of the coin: What is apishness, and when did the ape precursors become apes?) But for better or for worse, it is as legitimate to use the adjective "human" in the inclusive sense of being related to us by descent as in the exclusive one of applying only to creatures with all the qualities that distinguish us from the rest of the living world. Clearly, these two senses of the word are in conflict: an early member of our own group need not have possessed any of the qualities of the mind which we see as unique to ourselves—and certainly could not have had all of them. Indeed, it need only have possessed one or two of the anatomical novelties that *Homo sapiens* has acquired over the long course of its evolutionary history. Many anthropologists today would lean towards the inclusive use of the term "human" to embrace the australopithecines as well as later fossil members of the human group, but it is important to remember that (depending on the characteristics that you regard as being typically "human"), it might be difficult to view some of these members of the human family as "human" in a functional sense. Others would prefer to limit the descriptor to members of the genus *Homo*, or even to members of our species *Homo sapiens*; there is, alas, no definitive answer.

A Prophet in His Own Country...

Even as the outside world began to acclaim his discoveries, Broom was running into trouble back home in South Africa. Earlier in his career he had attracted the disapproval of his colleagues for supporting his paleontological research not simply by medical practice but by the sale of fossils to overseas institutions. Some rancour remained, and in the immediate postwar years this combined with concern for the ways in which Broom was recovering fossils from his cave sites. These localities were complex formations which had started life as subterranean cavities. They had filled up over long periods as debris of all kinds, including bones, fell in through shafts connecting with the surface. The stratigraphies within the cavities were clearly complicated, as were their subsequent histories of exposure at the surface due to erosion of the surrounding rocks; in certain quarters it was felt that the use of dynamite to blast apart the hard cave breccia was not the method of fossil recovery most conducive to the precise stratigraphic control needed if the fossils were to be reliably dated by faunal association. This concern was fair enough—if a bit overpunctilious given that the consolidated sediments were rock-hard—and, indeed, some degree of uncertainty over dating still mars our knowledge of every South African australopithecine site, though this can hardly be regarded as Broom's fault. But when the Historical Monuments Commission barred Broom from further work unless a "competent field geologist" participated, it was an egregious affront to one who had for years served as Professor of Geology and Zoology at Victoria College in Stellenbosch. Broom was outraged, and redoubled his efforts in defiance of the Commission (which ultimately relented). Within days, this paid off with the recovery of a virtually complete, if toothless, cranium at Sterkfontein, and by the end of 1947 Broom had amassed further specimens, including a lower jaw with teeth and a partial skeleton with a more or less intact pelvis (which showed pretty conclusively that its possessor had been an upright biped) and much of the vertebral column. These finds were monographed in 1950, by which time little opposition remained to Broom's interpretation of them as "types of ancestral man just a little more primitive than *Pithecanthropus*."

With undiminished vigor Broom shifted his attention in 1948 to another site in the neighborhood of Sterkfontein, this one known as Swartkrans. This has ultimately turned out to be among the most prolific sites of its kind, and Broom and his assistant John T. Robinson had hardly started work there before they began to find early human fossils. The first of these to come to light was an adolescent mandible of a robustly built form reminiscent of the one from Kromdraai; in 1949 Broom named this specimen *Paranthropus crassidens*, in celebration of its large chewing teeth, and before his death in 1951 he had recovered several crania of this species in varying degrees of completeness. The 1949 season also yielded a couple of jaws representing a more lightly built hominid that Broom and Robinson dubbed *Telanthropus* ('far man') *capensis*

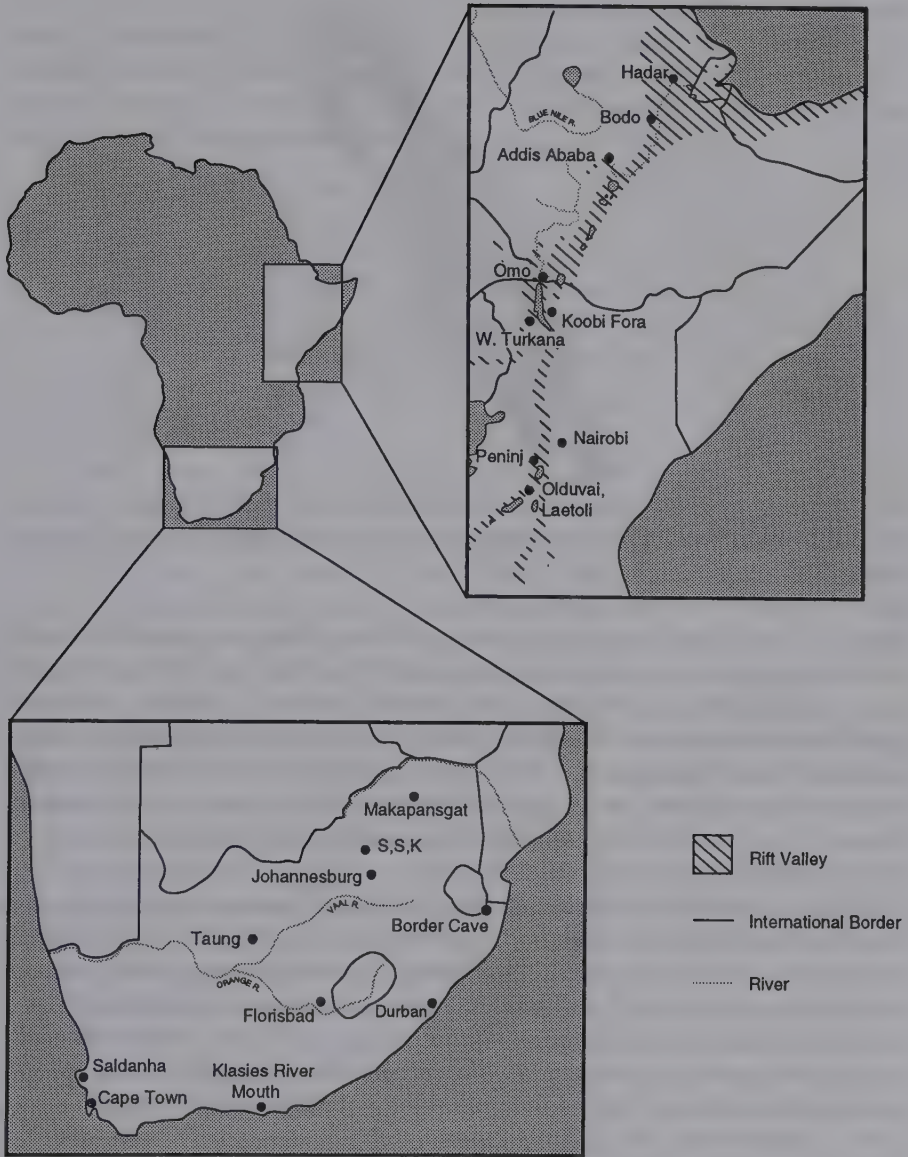


Front and side views of the cranium SK 46 from Swartkrans Member 1, South Africa, among the best-preserved remains of *Paranthropus robustus* (or *P. crassidens*). Scales are 1 cm. DS.

and considered to be “intermediate between one of the ape-men and true man,” perhaps comparable to the Mauer individual from Germany. Robinson subsequently allocated these new fossils to *Homo erectus*, as *Pithecanthropus* and *Sinanthropus* had both become known by the early 1950s. By the time that Robinson concluded his investigation of the site in late 1952, the considerable hominid collection from Swartkrans also included postcranial remains, including some hand bones and part of a pelvis. A few crude quartz artifacts were recovered from dumps of material removed by earlier lime miners, but they attracted rather little attention until later work at the site by C. K. Brain revealed a substantial stone tool assemblage in association with hominid remains.

African Genesis

Dart, meanwhile, had shown little inclination to pursue further paleoanthropological investigations—even though as early as 1925 fossils began to show up at other sites besides Taung. In that year a local schoolteacher, Wilfred Eitzman, had sent Dart some fossil bones from Makapansgat, a lime mine in the northern Transvaal. At the time Dart neglected to follow up on this opportunity, but in 1945 a team of archaeologists began working at the nearby Cave of Hearths. Among those excavating there was James Kitching, later to find fame as a finder and describer of Karroo reptiles. On his day off, Kitching wandered over to the now-abandoned Makapansgat limeworks and began picking through the lime miners’ dumps of cave breccia fragments. Fossils soon showed up in these rocky piles, and finally Dart decided to launch a field program at Makapansgat. During 1946 and 1947 a team led by the Kitching brothers and Alun R. Hughes sorted laboriously through the breccia dumps. This work



Map showing the locations of hominid-bearing fossil sites in southern and eastern Africa. S,S,K indicates the location of Sterkfontein, Swartkrans, and Kromdraai (and Drimolen). DS.

revealed another treasure trove of fossils, and thousands of mostly fragmentary bones were eventually recovered. Human fossils were not especially common among them (Ron Clarke—of whom we'll hear more later—once figured out that perhaps as few as eight hominid individuals were represented among the huge numbers of fossil fragments recovered), but they did include a partial



The MLD 40 half-mandible from Makapansgat Member 3, South Africa. Scale is 1 cm. DM.

cranium, several jaws, and some postcranial bones. These appeared to be more lightly built than the robust remains from Kromdraai and Swartkrans, and Dart allocated them to the new species *Australopithecus prometheus*, named for the Greek hero who stole fire from the gods. He did this in the belief that the blackened condition of many of the bones from Makapansgat showed that these creatures had used fire, much as Davidson Black had surmised at Zhoukoudian. It later turned out, however, that the blackening was in fact due simply to the deposition of manganese on the bones.

More significantly, Dart's analysis of the bone fragments suggested to him that these early humans had wielded what he called the Osteodontokeratic (bone, tooth, and horn) culture. Dart based this conclusion on the fragmentary condition of the mammal and other bones from Makapansgat and on the proportions of various body parts and animal species represented. He considered a number of possible explanations for the accumulation of bones within the cave and concluded that they could only have found their way inside, and have been broken as they were, as a result of hunting and butchering activities on the part of his *Australopithecus prometheus*. Many of the bone, tooth, and horn-core fragments, he believed, had been used as tools by these early humans, while the rest represented food remains. Further, Dart perceived similar patterns in the assemblages of animal bones recovered from Zhoukoudian and various European caves; this, to his mind, strengthened both his specific theory about the Makapansgat bone accumulations and his more general conclusion that osteodontokeratic tool assemblages had been widely used by early hominids.

This was pioneering work, even though later studies showed it to be in error, and it enabled Dart to make various suggestions about australopithecine

behavior. Some of these concerned the specifics of butchering techniques and dietary preference; other inferences were more wide-ranging, involving far broader aspects of intelligence, material culture, and behavior. The frequency among the bones of shattered crania and hoofs, for example, suggested to Dart the "focusing of australopithecine minds upon the sources of power," a

human trait [that] can only be interpreted by the man-like comprehension of *A. prometheus* that the heads and feet of animals embodied the animals' strength; and that this strength could not only be extracted from the animal but be assimilated to their victors, and be turned back upon the animals themselves for their undoing. The intellectual ability and manual dexterity displayed by the performance of these feats formed the background of their promethean culture.

What's more, "to that osteodontokeratic psychological indoctrination humanity added stone and metal but has never been able to free itself phylogenetically or ontogenetically from bone, tooth and horn." Seeing evidence for cannibalism in the way his australopithecine fossils were fragmented, Dart went on in his later writings, much less measured than Weidenreich's on Zhoukoudian, to characterize these creatures as bludgeon-wielding "murderers and flesh hunters," whose violent proclivities led inevitably to the "blood-spattered, slaughter-gutted archives of human history." Stirring stuff; and it certainly caught the imagination of popularizers such as Robert Ardrey, who in *African Genesis* and other books painted a picture of the bloody birth of mankind as a willful predator unlike any other: a marauding "killer ape" whose vicious disposition has passed to us intact.

Dart's extravagant claims predictably aroused lots of criticism, and later studies have shown that the Makapansgat bone assemblages more plausibly result from the combined activities of water and porcupines than from the predatory behavior of australopithecines. Nonetheless, they did feed into a general tendency of the time to substitute a cultural concept of what constituted mankind for the anatomical one embodied in such notions as Arthur Keith's "cerebral Rubicon." Interestingly, anatomists were among the foremost proponents of the idea that evidence for "human" status was best sought in behavioral evidence, preferably stone tools, properly the province of archaeologists. Weidenreich, for one, had as early as 1948 attacked Schepers' behavioral inferences from the brain casts of *Plesianthropus* with the declaration that "[c]ultural objects are the only guide so far as spiritual life is concerned." Solly Zuckerman took a similar tack: what mattered was not so much what the brain looked like, but what it was used for. All the inferences in the world about behavior were for naught in the absence of evidence of tool making—and stone tools, the benchmark, were lacking at that point from the South African sites. Ironically, then, Dart's claim that these human precursors indulged in the characteristically human activity of toolmaking was

coming under harsh criticism at the very moment when his insistence on the human, or at least prehuman, status of *Australopithecus* was becoming generally accepted.

Olduvai Gorge

Several thousand miles to the north, in East Africa, a shortage of stone tools was not Louis Leakey's problem. Born in Kenya to a missionary family, at the age of twelve Leakey was already collecting stone tools around his home near Nairobi. During his studies at Cambridge, he participated in a British Museum expedition to collect fossils in Tanganyika (now Tanzania) and thus added paleontological experience to his formal training in archaeology and anthropology. After graduating he led several archaeological expeditions to East Africa, gradually focusing his interest on Olduvai Gorge, a thirty-mile-long ravine cut into the Serengeti plains in northern Tanzania. The story goes that this chasm, in places as much as 300 feet deep, was discovered in 1911 when the German entomologist Wilhelm Kattwinkel almost fell into it as he chased butterflies across the Serengeti. Climbing down into the gorge, which cuts through many layers of sediments, Kattwinkel discovered large quantities of fossil bone lying around on the surface. The samples he took back to Germany caused a stir when it was found that they included parts of an early horse that had been extinct in Europe since the Pliocene, and a follow-up expedition was mounted in 1913 under the direction of Hans Reck of the University of Berlin. Reck's team collected large numbers of fossils and drew up a preliminary geological map of the gorge, but the find that attracted most attention was that of a human skeleton.

Later sediments accumulate on top of earlier ones, so when a pile of sediments is exposed by erosion, as occurs in the walls of the Gorge, the lower layers represent an earlier time than the higher ones. The skeleton was found fairly far down in the sequence of geological layers through which the Gorge was cut, and thus lay in sediments that were quite old, as the early Pleistocene mammal fossils found in the same layer seemed to testify. The anatomy of Reck's fossil human skeleton was modern, leading him to deduce that he had evidence for the very early existence of modern humans, much as Arthur Keith had lately concluded in the case of the Galley Hill skeleton. But, like Keith, Reck found himself assailed by colleagues who insisted that the skeleton was an intrusive burial into earlier deposits, and therefore testimony of no such thing. Clearly, further investigation was needed. But the First World War intervened, the British took control of Tanganyika, and the plans of German anthropologists to follow up on this suggestive find were thwarted. It was not until Leakey took one of his expeditions to Olduvai in the early 1930s that research there resumed.

One of the odd things about Reck's collection from Olduvai was that while it contained the remains of a perfectly modern human, it was completely

lacking in anything he could identify as a stone tool. Once Leakey arrived at the Gorge it became apparent why. Stone tools were actually there in abundance, but they were not made of the flint to which European archaeologists were accustomed. Flint is a perfect material for stone toolmaking because it fractures cleanly and predictably, producing sharp edges. But at Olduvai, and in East Africa generally, flint is lacking. Although small quantities of the volcanic glass obsidian were available in places, early East Africans had generally to make do with coarser, more granular materials. Such rocks—basalt, quartzite, and so forth—produce cruder, less fine-looking tools than flint, and the Germans had simply failed to recognize various unimpressive lumps of rock scattered around Olduvai for the tools that they were. With his eye locally trained, Leakey had no such problem. Arriving with Reck in 1931, he almost at once began to find tools. And just as Leakey had no trouble in persuading Reck that what he had found were indeed crude stone tools, once on the spot Reck seems to have had equally little difficulty in persuading the initially sceptical Leakey of the ancientness of his 1913 skeleton. Indeed, the presence of tools seems to have been the critical factor that changed his mind, and Leakey went on to document the occurrence of stone artifacts in all of the four major stratigraphic units of the Gorge, from Bed I at the bottom to Bed IV near the top. These, Leakey believed, showed a progressive evolution from crude “pebble tools” at the bottom (belonging to a culture he later termed the “Oldowan”) to handaxes at the top. Given the differences in raw material, these latter were remarkably similar to the handaxes of the Acheulean tradition Boucher de Perthes had recognized in France.

Later in the same year Leakey visited a couple of adjacent sites in western Kenya called Kanam and Kanjera. At the latter he found some unimpressive scraps of modern-looking braincase and at the former the front part of a rather battered lower jaw which he also assigned to *Homo sapiens* and which he claimed was older than the Olduvai skeleton. Back in England Leakey found his audience remarkably receptive to this ambitious though hardly well-substantiated contention, but it was not long before a distinguished geologist once more disputed the claim of great antiquity for the Olduvai skeleton. Leakey took this critic, Percy Boswell, with him on his next East African trip, in 1935, and to his great embarrassment found himself unable to substantiate his case. Nonetheless, he continued work at Olduvai, identifying a large number of artifact-yielding sites, making geological observations, and collecting large numbers of vertebrate fossils. At the end of the season, acting on a tip from a local Maasai, he visited some exposures nearby (relatively speaking; the trip from Olduvai took Leakey three days, though it's now about 90 minutes) at a place called Laetoli, and made a small collection of fossils there. These were believed at the time to be of about the same age as Beds I and II at Olduvai, and they included a hominid canine tooth, which remained unrecognized as such until 1981. The area was revisited in 1939 by the German explorer Ludwig Kohl-Larsen, who made a large collection of fossils that were

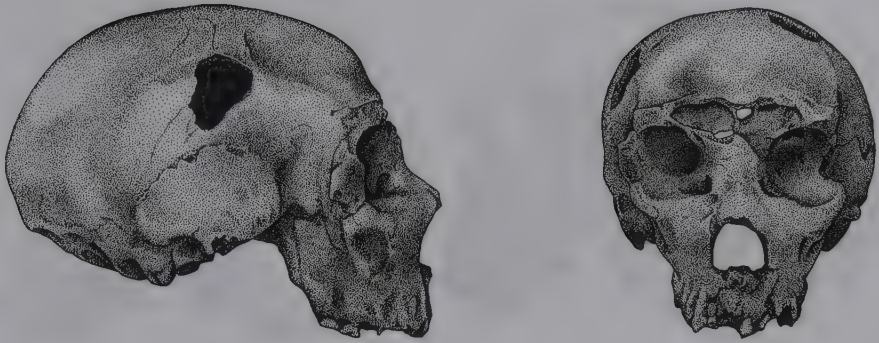
unfortunately derived indiscriminately from deposits of different ages. Among these fossils were a small piece of hominid upper jaw containing two teeth and an isolated molar that later served the paleontologist Hans Weinert as the basis for a new species, *Meganthropus africanus*. *Meganthropus* itself was a genus that had been set up by von Koenigswald to contain a massive fragment of lower jaw that had been found in the Sangiran deposits of Java. Laetoli was to figure importantly later on in the story of human evolution, but Leakey did not visit the area again until 1959, when remarkable news was about to emerge from Olduvai.

Still, back in 1935 the glory days of Olduvai were still a quarter-century in the future. The reputations of whizz kids are notoriously fragile, and Leakey's was severely dented by the debacle of the Olduvai skeleton, which was indeed a later burial into earlier deposits (to be precise, into the top of Bed II, after the overlying Beds III and IV had been eroded away). Combined with an acrimonious divorce in 1936, this placed an academic appointment in England beyond his reach, and from then on Leakey based himself in Kenya, working across the border at Olduvai as time and finances allowed.

Outside Africa

Elsewhere in the world, meanwhile, other finds were sporadically coming to light. In Europe, for instance, the two decades leading up to the Second World War saw the recovery of a number of new Neanderthal-like fossils. In 1926 the British archaeologist Dorothy Garrod recovered a juvenile Neanderthal skull from the cave of Devil's Tower in Gibraltar, and three years later a gravel quarry at Saccopastore, near Rome, yielded a quite lightly built Neanderthal skull that seemed to date from the last interglacial. It was accompanied by a variant of the Mousterian industry similar to that found at the somewhat later Italian site of Monte Circeo, where in 1939 a more typical Neanderthal skull was found in the center of what was described as a stone circle. Further afield, at about the same time, a partial skeleton of a nine-year-old Neanderthal boy was found at Teshik-Tash in Uzbekistan, allegedly buried within a circle of goat skulls. Dating of this specimen is still hazy, but it remains important in showing how far to the east humans of typical Neanderthal morphology spread during the later part of the Pleistocene.

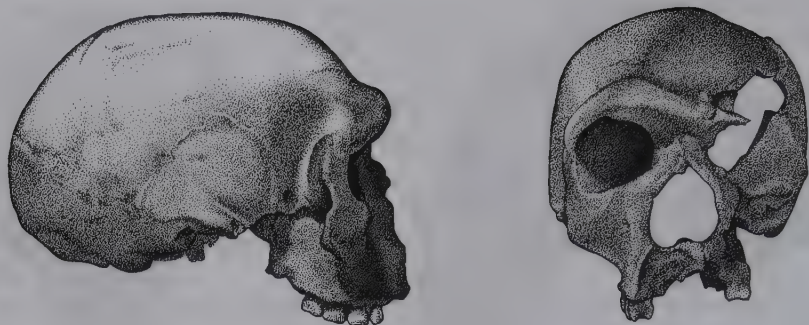
Less easy to interpret were the Swanscombe (England) and Steinheim (Germany) crania discovered in the mid-1930s. The latter was found in river gravels dated faunally to the second interglacial (Mindel-Riss), hence earlier than most if not all Neanderthal sites (though the original estimates placed it later). The specimen itself consisted of a reasonably complete if somewhat distorted cranium which was said to combine Neanderthal with more modern traits, despite a low estimated brain volume at about 1,100 ml. Neanderthal brain volumes, by contrast, were coming in regularly at about the modern average or possibly even a bit more. Arthur Keith suggested that the affinities of the



Side and front views of the Neanderthal cranium from Saccopastore, Italy. Scales are 1 cm. *DM.*

Steinheim skull lay with the Ehringsdorf specimen described by Weidenreich, which not all were happy to accept as a Neanderthal. The Swanscombe fragments seemed to be of about the same age and initially consisted of the occipital bone from the back of the skull and the associated parietal bone forming the left side; the right parietal was found twenty years later! Most judged at the time that the part of the skull preserved was remarkably modern looking, and the estimated brain capacity, at 1,325 ml, was well within the modern range. Keith declared this specimen to be a precursor of Piltdown, while others discovered more Neanderthal-like characteristics in the back of the skull.

Even more interesting and suggestive discoveries were being made in the Levant at about the same time. In 1925 a frontal bone with marked brow ridges but a relatively high forehead was exhumed by the English dilettante Turville Petre, along with a couple of other fragments of what may well have been a complete skull, from the cave of Zuttiyeh in Palestine (now Israel). It was found in association with a "Levalloiso-Mousterian" stone tool industry very similar to that of the European Neanderthals. As it happened, flint tools of this kind were also being picked up by visitors to the cave of Qafzeh, only a few miles away outside Nazareth. In the early 1930s these piqued the interest of René Neuville, the French Consul in Jerusalem, who began excavations in 1933. He rapidly uncovered an archaeological sequence that spanned the Middle and Upper Paleolithic. In the Middle Paleolithic (Mousterian) strata Neuville and his colleague Moshe Stekelis found fragments of five human skeletons, all of them anatomically modern. These were provisionally dated to the early part of the last glacial, but during Neuville's lifetime they remained undescribed and failed to attract the attention paid to those from the Mount Carmel sites. Indeed it is only very recently, with advances in dating techniques, that Qafzeh's full importance has been realized.

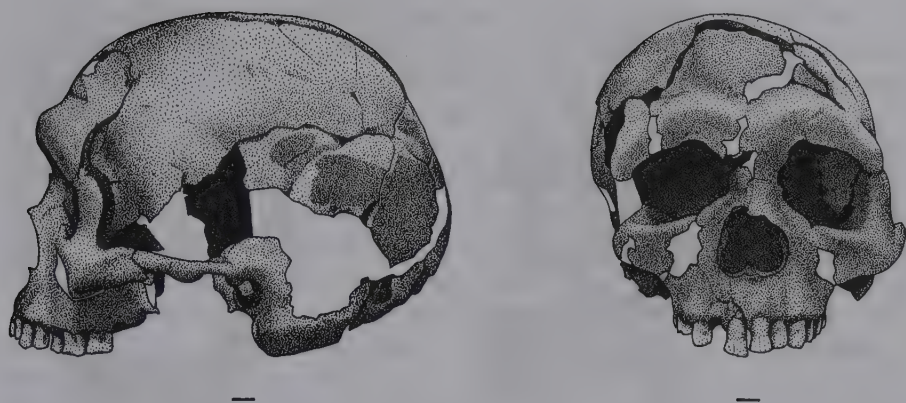


Side and front views of the distorted cranium from Steinheim, Germany. Scales are 1 cm. *DM.*

Much more influential at the time were excavations underway in limestone caves at the western foot of Palestine's Mount Carmel, in sight of the Mediterranean. Between 1929 and 1934 a team under the direction of Dorothy Garrod excavated the cave of Mughareet et-Tabūn, finding an almost complete female human skeleton and a more robust lower jaw interpreted as male. In the same layer were found numerous mammal bones, which appeared to date the humans to some time in the last interglacial period. While the female skull was more lightly built than those of most western European Neanderthals, and was also more rounded in the occipital (back) region, it otherwise possessed distinctly Neanderthal features. Once more, the associated lithic culture was Levalloiso-Mousterian. Nearby, in 1932 the same team excavated a virtual cemetery in the rock shelter of Mughareet es-Skhūl, where



Side and front views of the facial fragment from Zuttiyeh, Israel ("Galilee Man"). Scales are 1 cm. *DM.*



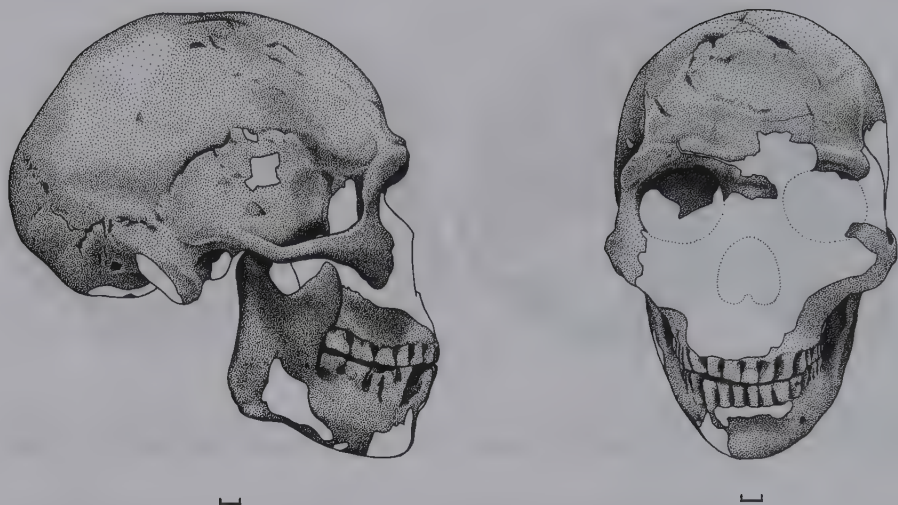
Side and front views of cranium 6 from Jebel Qafzeh, Israel. Scales are 1 cm. DM.

remains of at least 10 individuals of quite modern morphology were exhumed. The individuals of this population are unusual, among other things, in having distinct brow ridges; but although these structures do not at all resemble in form their counterparts in *Homo sapiens*, this has not prevented most recent authors from regarding them as essentially modern. Again, the stone tools from the site were Levalloiso-Mousterian; and despite certain faunal differences it was believed that the Tabūn and Skhūl populations were more or less contemporaneous, dating to the last interglacial.

The fossils from the two Mount Carmel sites were monographed together in 1939 by Theodore McCown and Arthur Keith, who described them as representing a single variable population. As good morphologists they clearly had difficulty in arriving at this conclusion, especially since the only anatomical basis they could find for it lay in similarities of the dentition. Significantly, it



Side and front views of the cranium C1 from Tabūn, Israel. Scales are 1 cm. DM.



Side and front views of the most complete hominid skull from Skhul, Israel (Skhul V). Scales are 1 cm. DM.

appears that McCown and Keith felt obliged to group these fossils principally because they shared similar lithic industries. Further, the two sites were only a stone's throw from each other and were, they believed, of about the same age. This made it necessary to explain why a population containing humans as different as those from Tabun and Skhul should be so extraordinarily variable. Were these people "in the throes of an evolutionary transition and therefore unstable and plastic in their genetic constitution?" Or "is the variability due to hybridity, a mingling of two diverse peoples or races?" McCown and Keith eventually came down in favor of the former explanation, though others have leaned towards the latter. In any event, by evoking these two possibilities, McCown and Keith set the parameters for discussion of the Mount Carmel people for years to come.

In comparing the Mount Carmel assemblage with others known, McCown and Keith clearly faced a difficult situation, lacking as they did a homogeneous assemblage. They saw a spectrum of late Pleistocene fossil humans, with one extreme represented by the European Neanderthals and the other by the Cro-Magnons. In the middle lay Mount Carmel, with the Tabun types closer to the former, the Skhul ones to the latter. Between the Tabun variety and the "classic" Neanderthals of western Europe lay the Krapina people from Croatia, representing a more lightly built intermediate variant, while the Skhul and Cro-Magnon forms were considered very close indeed to each other, both showing specifically European characteristics. But instead of concluding from this perceived continuity of form that the Neanderthals had simply evolved into modern Europeans via a Mount Carmel-like stage, McCown and Keith proposed a more complex scenario. Noting that Neanderthals were

ubiquitous in western Europe during the "middle Pleistocene," but that this type became progressively modified from west to east until in Palestine there appeared a type transitional towards the modern, they extrapolated this trend to suggest that the ancestors of the modern European population had arisen in western Asia somewhere to the east of Palestine. The Mount Carmel people themselves were therefore "not the actual ancestors of the Cromagnons but Neanderthaloid collaterals or cousins of that type." It took me several readings of McCown and Keith's breathtakingly opaque presentation to grasp this reasoning, and this lack of crystal clarity provides, I think, a good example of what happens when you allow yourself to be persuaded by factors other than morphology in making decisions as to evolutionary relationship. Or perhaps it merely reflects what happens when two authors cohabit rather uncomfortably between the covers of the same monograph. Whatever the case, Weidenreich was delighted by McCown and Keith's declaration that "Eastern Asia [was] the cradle of the proto-Mongols," and as a reciprocal courtesy he added Palestine to his list of centers of the evolution of modern humans, the Near East becoming the source of modern Europeans.

CHAPTER 7

The Synthesis

Although you don't have to wander far if at all beyond the confines of the Order Primates to find examples of virtually the full spectrum of evolutionary phenomena, it remains true that anthropology has contributed rather little to the general development of evolutionary and systematic theory. Indeed, it's probably fair to say that paleoanthropology has typically been a consumer rather than a producer of useful evolutionary theory. Perhaps it's not entirely surprising, then, that it took a while for paleoanthropology to feel the effects of a profound transformation of evolutionary thought that took place during the 1930s and 1940s. During these years Broom could on the one hand agree with Alfred Russel Wallace that "the large brain could not have arisen by Natural Selection," and von Koenigswald could insist on the other that size increase was inevitable—while neither claim sounded particularly odd to anthropological ears. Yet, well before these sages wrote, the foundations had already been laid of what was rapidly (except, perhaps, in France) to become an evolutionary orthodoxy that has lasted up to our own day.

By the 1920s and early 1930s the fragmentation of evolutionary biology to which I've already referred had become downright chaotic. Almost everyone had his own theory of evolution, and few of these were Darwinian in the sense that natural selection was accepted as the prime force behind evolutionary change. Antiselectionism was, indeed, the order of the day. Many biologists, including anthropologists such as Weidenreich, were still infected to one extent or another by the concept of orthogenesis, the idea that evolution was directed by an inner drive towards a fixed goal. A variant of this idea held that evolutionary change was the expression of some kind of innate potential that lay within each lineage of organisms. Saltationism was still rife, whereby new kinds of organisms were seen as arising abruptly by some mechanism of discontinuous variation. "Mutations" were often viewed not as the small genetic alterations to which we refer by this term today, but as quantum changes giving rise to new species; it was, indeed, in this sense that Hugo de Vries had coined the term back at the beginning of the century. And where mutations were spoken of in the modern sense, it was often concluded that "mutation

pressure" was a driving force of evolution. Various forms of Lamarckian thought were also current, among them the ideas that environmental changes somehow induced changes in the organism, or that use or disuse of organs during the life of an individual controlled how those organs would appear in its offspring. Even some avowed Darwinians incorporated elements of such thinking in their evolutionary theories, combining natural selection with ideas of "soft"—broadly, Lamarckian—inheritance. Weissmann's demonstration of the separation of germ line (genes) and soma (body) had yet to become accepted throughout biology, although decades before it had instantly been absorbed by Wallace and several others to produce a "neo-Darwinian" school of thought.

Moreover, as the ornithologist Ernst Mayr has chronicled in several fascinating historical accounts, the first third of the twentieth century witnessed divergence to the point of alienation between the varied disciplines which we think of today as parallel branches of evolutionary biology. The geneticists pursued their genes, often using fruit flies as their experimental models; the zoologists sought the nature of species and the mechanisms of their origin; and the paleontologists applied themselves to the description and classification of the species of which the rapidly growing fossil record was composed. Between these various specialties, then, there rapidly developed some pretty massive barriers of mutual incomprehension. In 1944 the paleontologist George Gaylord Simpson, Mayr's colleague at the American Museum of Natural History, characterized this situation in a famous passage:

Not long ago, paleontologists felt that a geneticist was a person who shut himself in a room, pulled down the shades, watched small flies disporting themselves in milk bottles, and thought that he was studying nature. A pursuit so removed from the realities of life, they said, had no significance for the true biologist. On the other hand, the geneticists said that paleontology had no further contributions to make to biology, that its only point had been the completed demonstration of the truth of evolution, and that it was a subject too purely descriptive to merit the name "science."

Perhaps such attitudes resulted fairly inevitably from what seemed to be rather fundamental differences in preoccupation. Apart from a rearguard action against the waning advocates of soft and "blending" inheritance, the stuff of the genetics of the time was the study of how the frequencies of different alleles within populations might change given mutation both at the level of the gene and at that of the chromosome, where it was coming to light that mix-ups involving whole strings of genes could also occur. And there was no evident relationship between gene frequency (or "microevolutionary") change and the "macroevolutionary" phenomena that were of primary interest to naturalists: the origin of species, the existence of higher taxa, evolutionary diversity, and so forth. Mayr eventually pointed out that in fact all of these elements actually belong to a single hierarchy that runs from molecules and

genes, through individuals, populations and species, to higher taxa and associated macroevolutionary phenomena; part of the problem arose because the geneticists were looking at the lower levels of the hierarchy while the naturalists were interested in the higher ones. But part only: the rest lay in such things as the tenacity of saltationism and the refusal of soft inheritance to go away, factors that also did much to ensure that even within each major field of study discord was the order of the day.

A Remarkable Convergence

On the face of it, this was hardly fertile ground for agreement within disciplines, let alone among them; yet by the mid-1940s a "synthesis" had been achieved in evolutionary thought to which almost everyone subscribed. The emerging "Evolutionary Synthesis," as it became grandly termed, was initiated by some sophisticated mathematical modeling, beginning in the late 1920s, by such luminaries of population genetics as Sewell Wright in America and Ronald Fisher in England; and it became encapsulated in a series of books by more hands-on biologists that began to appear in the late 1930s. The Synthesis was an attractive and ultimately highly reductionist formulation, involving the integration of Darwinian ideas of natural selection with changing frequencies of genes in populations. Perhaps the neatest early demonstration of how this might be done was the idea of the "adaptive landscape" first put forward by Sewall Wright in 1932. As visualized at the time, the hereditary material—the genes—is strung out along the chromosomes. Each gene occupies a particular spot or "locus" on its chromosome, at which it may be represented by one of several different alternative forms, known as "alleles." With many thousands of loci, each with several alleles, the "gene pool" of any population contains vast numbers of different combinations of alleles, or "genotypes." Some of these, surmised Wright, had to be more favorable than others, producing "fitter" individuals better able to survive and reproduce in any given environment. He drew the equivalent of a topographical map in which the contour lines connecting areas of equal elevation were replaced by lines delineating regions of fitness. On the hilltops were clustered the fitter genotypes, while the less fit genotypes occupied the valleys. On this analogy, the major problem for each species was to maximize the number of individuals occupying the hilltops and to populate the valleys as little as possible. This was a powerful analogy, and essentially a Darwinian one, even though Wright clearly recognized the importance of chance factors ("genetic drift") in affecting the survival of new alleles or gene combinations. The relative fitness of individuals was, of course, the central heritage of Darwinism and virtually implied natural selection.

The adaptive landscape metaphor was rapidly picked up and elaborated upon by many different people, often way beyond Wright's original intentions. The peaks, particularly, came to represent many different things. But however it is interpreted, this analogy clearly marries selection and gene frequencies,

and it is this combination which set the scene for developments to come. Many different scientists contributed to Synthesis, but the major coherent statements of its principles appeared in three books. The first and most seminal of these, the geneticist Theodosius Dobzhansky's *Genetics and the Origin of Species*, appeared in 1937; Mayr followed up in 1942 from the systematist's viewpoint with *Systematics and the Origin of Species*; and Simpson brought paleontology into the fold in 1944 with *Tempo and Mode in Evolution*. Each of these works obviously had its own particular focus, but all accepted the same basic principles. First, evolution was a gradual, long-term process, essentially consisting of the accumulation within lineages of small genetic mutations and recombinations. Over enough time, the accumulation of minor changes would result in large effects. Second, this generation-to-generation change was controlled by natural selection, environmental factors promoting adaptation within the lineage via the differential reproductive success or failure of different variants. As environments changed, populations would change to keep in step and maintain or improve their adaptedness. Third, this same process of the gradual accretion of genetic (hence physical) change could be extrapolated to explain higher-level phenomena, such as the origin of new species and of biotic diversity.

It was agreement on this last point that was crucial in bringing together those who studied genes and those whose central interest was organisms. For while the gradual accretion of genetic change implied a basic continuity, it was nonetheless evident to anyone concerned with the world of living organisms that the biota is marked by discontinuities: each species in the marvelously varied living world was a more or less isolated genetic package, distinct from all others. If the basic mechanism of evolution was simply one of small changes summing up over time to produce major effects, where did these discontinuities come from? The adaptive landscape had the answer. Its peaks were favorable ecological niches, to which their occupying populations were adapted. In contrast the valleys between were hostile areas, and no individual of a species could afford to slide too far down the slope toward the valley floor. But the map didn't stay constant: as Simpson put it, it was "more like a choppy sea than a static landscape." Natural selection had to operate incessantly to keep each population nicely balanced on the peak that was shifting beneath it, and from time to time a peak itself would divide, giving rise to two peaks, which then moved apart. With natural selection working in different directions on each new peak, in time the occupying populations, once one, would have diverged enough to be separate species. Presto! Speciation—the production of new species—was reduced to another aspect of adaptation, itself founded on the slow accumulation of tiny genetic changes. And repetition of this simple process over long periods of time would ultimately give rise to new genera, families, orders, and on up. Among mammals, at least, this meant that speciation was unlikely to occur without some external barrier (a seaway, a desert, a mountain range) dividing a widespread population into two. But once that had occurred, the result was almost a foregone conclusion.

This was, of course, great for the geneticists, and particularly for the mathematical modelers among them. For it meant that the key to evolutionary change was entirely held by the guardians of the nascent and model-oriented science of population genetics. It was also fine for the zoologists, who, while having to concede that species were not discrete packages in time, were still able to view them as discrete in space, which was what counted in their day-to-day business. But it was awkward for the paleontologists. It is tough to be a scientist without a basic conceptual unit of study, and the Synthesis had robbed paleontologists of this fundamental necessity—for it is certainly not provided by the individual fossil (unless that fossil happens to be the only one of its kind that you have). The first thing you need to know about any fossil, before you can fit it into any larger picture, is “What species does it belong to?” And under the Synthesis, species inexorably evolve themselves into other species by constant tiny incremental changes. Over time, which is the unique property of the fossil record, species lose their identity: it is impossible to say where any one starts or finishes. Lineages, ancestor-descendant sequences of populations in the fossil record, may undergo enormous quantities of change from their beginnings to their ends. And any member of that sequence *must* have belonged to a particular species. But the lineages of which those species are components can only be divided up in an arbitrary manner; and beyond depriving paleontology of a theoretically rigorous structure, on a practical level this creates the potential for unresolvable disagreement. It is for this latter reason that post-Synthesis times witnessed the undignified spectacle of paleontologists congratulating themselves on the deficiencies of their data base: the famous gaps in the fossil record, it was said, provided handy places at which to break up lineages into segments that could conveniently be labeled with species names in the same way as is done with living forms.

Small wonder, then, that rethinking of the claims of the Synthesis to be a comprehensive explanation of the evolutionary process was ultimately to come from students of the fossil record. But there is no question that the architects of the Synthesis had produced a magisterial achievement that swept away a huge panoply of evolutionary mythology. Gone were ideas like orthogenesis and saltationism, replaced definitively by Darwin’s original concept of evolution as an opportunistic, non-goal-oriented process. In no field was this development more salutary than in the study of human evolution, where the temptation to produce orthogenetic or finalistic interpretations had been particularly strong, and where reluctance to abandon them was commensurately marked. And the triumvirate of the synthesis showed no reluctance to share the benefits of their insight with their paleoanthropological colleagues.

Population Thinking

The synthesis had been born of the emergence of what Mayr called “population thinking.” Many early geneticists thought of species in terms of sets of

particular intrinsic qualities, while systematists—those concerned with the description and analysis of the diversity of life—had traditionally been prone to regard species as types. It was recognized that species consisted of large numbers of individuals, but each individual was thought to conform more or less to a basic archetype. Population thinking, in contrast, involved the realization that species consisted of clusters of unique individuals and populations and that there was no ideal “type” against which any individual could be measured. This opened the door to a whole new view in which local populations played a critical role in the production of new species and new adaptations. Most species were “polytypic,” composed of several such populations, each one an aggregate of unique individuals and with its own geographical range. Each, too, differed slightly on average from the next, so that distinctive populations might not represent the separate species that a typologist would recognize. The critical test was not external form, but reproductive continuity. The synthesis recognized such geographically varying local races, or subspecies, as the engines of evolutionary change.

As early as 1944 Dobzhansky applied this kind of thinking to the human fossil record and concluded that “the differences between Peking and Java men are easily within the magnitude range of the differences between the living human races.” Further, rejecting the conclusion of McCown and Keith, he found that the variability among the Mount Carmel fossil humans must have been due to hybridization between Neanderthals and moderns, two subspecies that had arisen elsewhere but which, belonging to the same species, had interbred on encountering one another. Ignoring a certain amount of circularity in his reasoning, Dobzhansky declared that the Mount Carmel people showed “how rash are the assertions of some writers that in fossil forms evidence on presence or absence of reproductive isolation can never be obtained!” From this he proceeded to the conclusion that, “in Hominidae, a morphological gap as great as that between the Neanderthal and the modern may occur between races rather than species,” although it remained for him an open question whether Peking/Java and the Neanderthals were distinct species or only racially separate.

Dobzhansky then discussed what he considered the two leading current models of human evolution. On the one hand there was the “classic” view, which “produced a tree with many branches...[of which] the known fossils represent...only rarely the main phylogenetic trunk,” and on the other there was Weidenreich’s “parallel development of races,” whereby several distinct racial lineages separately passed through the same general series of evolutionary stages to achieve modern form. Finding (unsurprisingly, given the amount of intraspecific variation he was prepared to accept) that “as far as [is] known no more than one hominid species existed at any one time level,” Dobzhansky envisioned a highly complex set of local developments and hybridizations among human populations throughout the Pleistocene. But he concluded that the differences between the two hypotheses before him were hardly significant given that pretty much the entire set of human evolutionary

developments since Java Man had taken place within the confines of a single polytypic species. And although he was undoubtedly right to attack the typological approach to classifying fossils in the human record, in deliberately brushing complex events beneath the single-species rug Dobzhansky was fostering what may be the most destructive canard in the entire long catalog of paleoanthropological misconceptions.

Not that his fellow Synthecist Ernst Mayr had any objections. At an influential conference held at Long Island's Cold Spring Harbor in 1950 (at which Simpson still felt compelled to reiterate the arguments against such anachronistic beliefs as orthogenesis and the inevitability of size increase over time), Mayr tried to bring the naming and classification of fossil humans into what he saw as equivalence with those employed in other areas of zoology. Blown up to human size the 600 species of *Drosophila* fruit flies would, Mayr claimed, look very much more different from each other than do humans and gorillas, or even monkeys. The fact that many distinctive populations formerly classified as separate species were now recognized as mere racial variants meant that we had to adjust our categories all the way along the line. While the chimpanzee and gorilla were clearly good species, Mayr said, they equally clearly did not deserve to be classified in separate genera. Similarly, there was no justification for separating the apes into a family (Pongidae) distinct from that of humans (Hominidae); and as for the australopithecines, well, they all belonged to the same genus. And this genus might, indeed, even be our own *Homo*, since upright posture (which freed the hands, which in turn stimulated development of the brain) had been achieved. In the end, Mayr plumped for placing all known fossil humans in the genus *Homo*, within which he recognized the three species *H. transvaalensis*, *H. erectus*, and *H. sapiens* (including Neanderthals).

Like Dobzhansky, Mayr could find no evidence for the existence of more than one human species at the same point in time, despite accepting the about-to-be-exposed Piltdown remains (which Dobzhansky had dismissed as a fortuitous association of human and ape fossils) as a genuine combination. He explained loftily that the difficulties Weidenreich and others had experienced in reaching the same conclusion were simply due to their inability to comprehend that "one type does not change into another type evenly and harmoniously, but that some features run way ahead of the others." This rash assertion did nothing to diminish the influence of Mayr's analysis, and his paper ushered in among paleoanthropologists, if haltingly at first, an era of "lumping" (minimizing the number of taxa recognized), that was sharply at variance with the older "splitting" tradition derived from typology and the human anatomical tradition.

Paleoanthropology Capitulates

During the 1950s new technologies were filtering into paleoanthropology as well as new ideas on how evolution might be expected to occur. One of

these was fluorine analysis, a technique first floated in the mid-nineteenth century but only seriously applied a hundred years later by Kenneth Oakley at the British Museum (Natural History). Fossils take up fluorine from the surrounding deposits at a steady rate. Thus, in theory, if you know how much fluorine there is in a fossil, you will also know how long it has been buried. In practice it turns out that fluorine content is affected by too many variables to provide a reliable general dating system. However, fossils that have been buried in the same place for the same length of time should indeed contain the same concentration of fluorine. And this obviously provides a means for determining whether two specimens found in the same stratum are contemporaneous. It was, indeed, the application of fluorine analysis to the Piltdown specimens that precipitated the exposure of the fraud: the fossils of extinct mammals that had accompanied *Eoanthropus* contained high levels of fluorine, up to about 3%, while specimens attributed to the human form averaged an insignificant 0.02%. But perhaps as importantly, fluorine analysis and similar methods proved for once and for all that Galley Hill and other putatively ancient humans of modern anatomy represented intrusive burials into the deposits from which they had been recovered.

Thus, at mid-century, a clearing-out process was in progress that swept away not only a large accumulated burden of discredited evolutionary theories, but a whole suite of pseudo-fossils whose presumed great age had made nonsense of rational efforts to understand the human fossil record. One of the first paleoanthropologists to capitalize on these new developments was F. Clark Howell, then of the University of Chicago, who reanalyzed the Neanderthals in 1951. With such awkward forms as Piltdown and Galley Hill eliminated from consideration, he was able to envisage a single lineage in Europe that led from Mauer through Swanscombe to Steinheim and thence to an "early Neanderthal" assemblage to which such forms as Ehringsdorf and Saccopastore belonged. These forms seemed to date from the last (Riss-Würm) interglacial and to have shorter, higher, generally more lightly built skulls—hence more like modern humans—than the later "classic" Neanderthals (Neanderthal, La Chapelle-aux-Saints, La Ferrassie, Monte Circeo, et al.) of the last (Würm) glacial. Howell also saw a geographical trend, the early Neanderthals from sites in western Europe tending more toward the "classic" condition than those from further east (Krapina, Mount Carmel). From these distributions in time and space flowed the idea that early Neanderthals in eastern Europe and the Levant had given rise, via the Mount Carmel assemblage, to modern humans; toward the west, in contrast, slightly different early Neanderthals had given rise to the "classic" forms. Howell rejected the possibility of hybridization between classic Neanderthals and moderns because the evidence pointed so clearly to abrupt replacement in western Europe of the former by the latter.

This scenario made excellent sense both in terms of the dictates of the Synthesis and of the increasingly detailed record of Pleistocene glaciation

that geologists were compiling in Europe and western Asia. During the mild climate of the Riss-Würm interglacial, an early Neanderthal population was widespread across this region, with members of its western portion foreshadowing more strongly than those to the east the physical peculiarities of the "classic" form. With cooling of the climate as the Würm glaciation began, the western population became effectively cut off from that to the east as the Scandinavian, Alpine, and Pyrenean ice sheets expanded and converged, and conditions deteriorated in the corridors between them. Subjected to a harsher climate than their relatives to the south and east, and consequently to a severe regime of natural selection that was perhaps aided by genetic drift in small populations, the more or less isolated Neanderthals of western Europe acquired their exaggerated "classic" specializations.

In 1952 Howell looked more closely at the faunas accompanying the various Classic Neanderthal finds and concluded that, to the extent to which it was possible to judge, all were approximately contemporaneous, dating from the first part of the Würm glacial. Only with the beginning of an "interstadial"—a period of warmer climate within the glacial—did archaeological and later fossil evidence begin to appear of the occupation of western Europe by modern humans, by which time the Neanderthals had vanished, perhaps with the disappearance of the environment to which they had so closely adapted, or maybe because they were "extinguished" by their modern cousins as they arrived from an eastern place of origin. In some way I find hard to define exactly, but that probably has much to do with their infusion by the spirit of the Synthesis and the discounting of Piltdown et al., these two papers by Howell seem to me to have inaugurated what one might call the "modern" era of paleoanthropological studies.

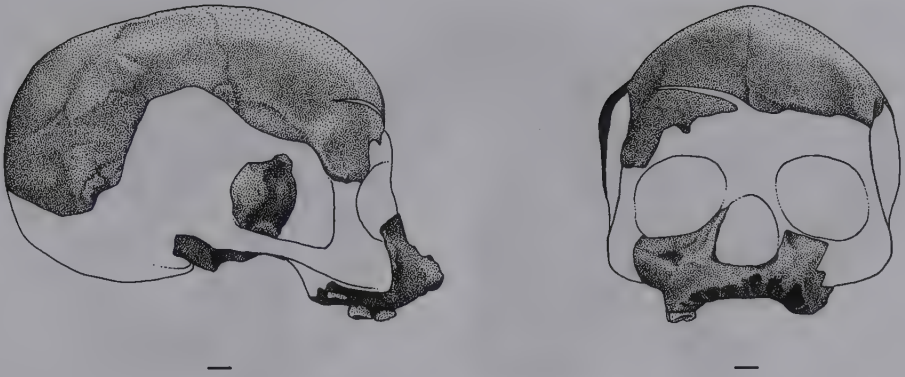
Radiometric Dating

Another measure of modernity was lacking, however. As this century passed its midpoint, there were still no practical ways of determining the absolute ages—ages in years—of fossils. Dating was relative: this geological layer underlies this other one, therefore it is older; these extinct animals are found in older layers, while these others are found in younger ones; that site is older than another because it contains an older fauna. And although the labors of geologists and paleontologists over the decades had produced remarkably detailed local and worldwide relative chronologies, there was still no way to calibrate these in terms of the passage of years. A sort of calibration had been tried in terms of sedimentation rates—the rates at which sedimentary rocks are laid down—which is why many early evolutionary trees incorporated the depths of sediment characteristic of various periods much as we use time-scales today; but it took the arrival of methods of absolute dating to show just how approximate and unreliable such extrapolations were.

The first method of absolute dating to be introduced was the radiocarbon (carbon-14: ^{14}C) technique, invented by Willard F. Libby in 1950. This, like most later methods, depends on the phenomenon of radioactivity, which is why such dating is often known as “radiometric.” Many naturally occurring atoms (the radioactive ones) possess unstable nuclei that spontaneously “decay” to stable states of lower energy. When a radioactive “parent” atom decays, it changes to another type of atom known as the “daughter” product. The rate at which it does this is effectively independent of external conditions and is characteristic of the particular kind of atom involved. In theory the time that it will take for all parent atoms in a system to decay is infinite, so rates of radioactive decay are expressed in terms of a “half-life,” or the time it takes for half of the atoms in a system to decay.

The radiocarbon technique depends on the decay of ^{14}C , an unstable form of carbon that is incorporated as a small but constant percentage of the carbon that all living things contain. When an organism dies its ^{14}C ceases to be renewed and begins to decline by decay as a proportion of total carbon present. Measuring the amount of ^{14}C relative to stable carbon contained in an organic sample thus provides a way of finding out how much time has elapsed since the death of the organism concerned. At 5,730 years the half-life of radiocarbon is relatively short, so that when a sample is more than about 40,000–50,000 years (40–50 kyr) old it contains an unmeasurably small amount of radiocarbon. This obviously places an effective limit on the usefulness of the method—although during the early days hopes were high that isotope enrichment techniques would extend its range by a few tens of thousands of years, and several very ancient dates, generally viewed with suspicion, were published. Another limitation was, to begin with, the size of the sample needed for effective measurement: besides considerable technical difficulties in using most fossil bone, you needed to destroy a large chunk of it to get a date. Obviously, people didn’t want to lose their precious human fossils in the process of finding out how old they were; so radiocarbon dates were typically obtained on organic materials (charcoal was a favorite) associated in the same deposits as the human fossils, at least until the relatively recent advent of a variation known as AMS dating, which requires only tiny samples.

Given the 40 kyr maximum of radiocarbon dating, this method was clearly going to be restricted to the latest part of the Pleistocene. Early results thus didn’t send shock waves through paleoanthropology, for everyone was pretty sure that they were dealing in this period only with tens of thousands of years. But the new precision that radiocarbon permitted was exquisite, and archaeologists, particularly, were entranced. One of the earliest to capitalize on this new tool was Harvard’s Hallam Movius. In 1954 he obtained a date of around 24 kyr for Gravettian layers at the Abri Pataud, a rock shelter in Les Eyzies which he was then excavating; and before long he was able to propose a rough timescale for the latter part of the last glacial in western Europe. Mousterian artifact assemblages, more or less exclusively associated in that part of the



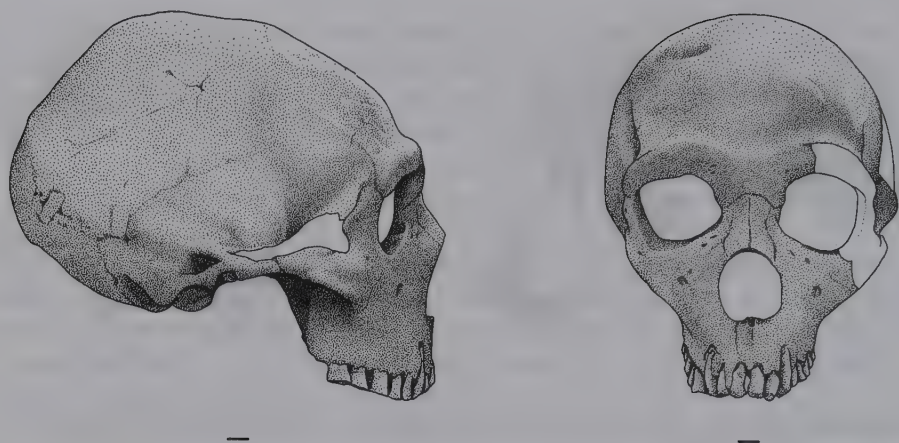
Side and front views of the early modern human skull from Niah Cave, Sarawak. Scales are 1 cm. DM.

world with Neanderthal physical types, started well outside the range of the radiocarbon technique, and persisted up to about 32 kyr. What is now known as the Châtelperronian industry, then variously interpreted as the work of late Neanderthals or early moderns, began somewhat earlier than this and ran to about 30 kyr. The Aurignacian, the first undisputed Upper Paleolithic industry, began at around 32 kyr, while the end of the Pleistocene, which coincided broadly with the disappearance of the high cultures of the Upper Paleolithic, occurred at around 10 kyr.

It was thus clear early on that nonmodern human fossils were only likely to be found toward the outer limit of the radiocarbon technique; and in any event, because sites yielding human fossils are much rarer than sites with artifacts, dates associated with actual human fossils were generally slow to come in—although a calibrated archaeological record went a long way toward providing the needed timescale for the latest phase of human evolution. Perhaps the first chronometric dates for fossil humans were obtained in 1951 by Junius Bird of the American Museum of Natural History for specimens from South America; but these dates were post-Pleistocene, if only just, and dates directly associated with nonmodern humans began to accumulate significantly only during the 1960s. Perhaps the most intriguing radiocarbon date to emerge during the 1950s came from the Niah cave in Sarawak, where in 1958 charcoal found in deposits just above the skull of a young modern male was dated to just under 40 kyr. This was considerably earlier than any presumed occurrence of modern humans in Europe, which led to doubts about the veracity of the date, although today it is considered pretty reliable.

The Record Expands and Stereotypes Fall

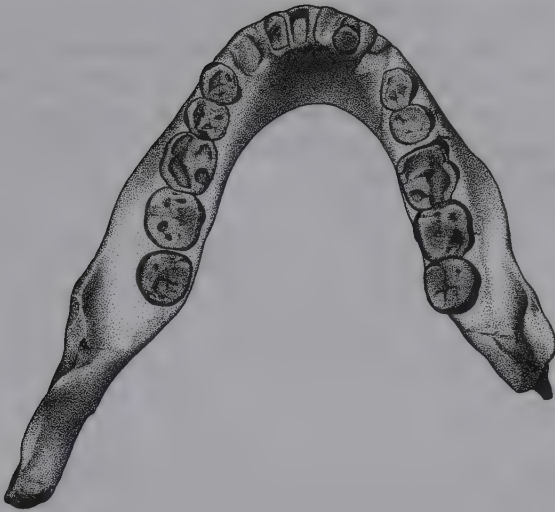
The 1950s also witnessed the discovery of a number of significant new human fossils besides those from South Africa already mentioned. Between 1953 and



Side and front views of the Shanidar 1 cranium from Iraq. Scales are 1 cm. *DM.*

1957 the archaeologist Ralph Solecki recovered the remains of nine adult and juvenile Neanderthals, associated with a Mousterian industry, from Iraq's Shanidar cave. One of these skeletons was that of an adult male who had suffered, perhaps since birth, from a disabling disease that had deprived him of the full use of his right arm. Without the support of his social group he could not have survived, but he succeeded in living to an estimated age of 40, an old man by Neanderthal standards. Pollen grains beneath another skeleton suggested that it had been buried with flowers, though this has since been disputed. Anatomically and stratigraphically the Shanidar population fell into two groups, specimens from higher in the section allegedly having more "classic" features, while those from lower down resembled other members of Clark Howell's eastern group in lacking dramatically swept-back cheekbones. Radiocarbon dates made in the late 1950s and early 1960s placed the Shanidar Neanderthals at or beyond the outer limit of the technique; the earlier ones are believed today to date from about 70–80 kyr and the later ones from about 50 kyr.

But quite as important as new Neanderthal finds in the 1950s was the recognition, finally, that the stoop-shouldered, bent-kneed stereotype of these humans created by Marcellin Boule was totally false. Hints to this effect had appeared in the literature over the preceding decades, and in 1955, independently, both the Swiss primatologist Adolph Schultz and the French paleontologist Camille Arambourg stated explicitly that the Neanderthals must have walked fully upright. Schultz noted that the Neanderthal head had been balanced perfectly atop the vertebral column, and pointed to the inherent instability of the posture that the Neanderthals were supposed to have adopted. Arambourg looked at various features of the skeleton of the "old man" of La Chapelle-aux-Saints studied by Boule, and found no evidence for the latter's disparagement of the Neanderthals. This showed, he declared, that uprightness



One of the “*Atlanthropus*” (*Homo mauritanicus*) jaws (Ternifine 1) from Tighenif, Algeria. Scale is 1 cm. DM.

had to be total to work at all. It’s rumored that Arambourg’s defense of the Neanderthal was precipitated by his discovery of “Neanderthal-like features” in an X-ray of his own neck; and whether this is true or not, Schultz and he were totally vindicated in 1957 when the anatomists W. L. Straus and A. J. E. Cave published a detailed reanalysis of the La Chapelle-aux-Saints skeleton.

It turned out that this individual, which had become the stereotypic Neanderthal, in fact showed both osteoarthritic degeneration (which Boule had actually been aware of) and changes due to age. As important, many of the differences from modern humans to which Boule had pointed were in fact not differences at all, once the range of variation in modern human populations was taken into account. Indeed, like Arambourg, Straus and Cave could find nothing at all in the skeleton to indicate that its owner had not been a perfectly efficient upright biped. Certain differences there were between Neanderthals and modern people, in the postcranial skeleton as in the skull, but they certainly did not reflect any lack of a fully upright posture.

Arambourg was involved in a further find of importance made during the 1950s: the discovery in 1954–55 of three quite large-toothed lower jaws, some teeth, and a small skull fragment at the site of Tighenif (then Ternifine) in Algeria. In association were found both handaxes of Acheulean type and flaked pebbles, and a fauna that seemed to indicate an early Middle Pleistocene date. Although Arambourg described the human fossils as belonging to the new genus and species *Atlanthropus mauritanicus* (the synthesis and population thinking took an awfully long time to catch on in France), they soon

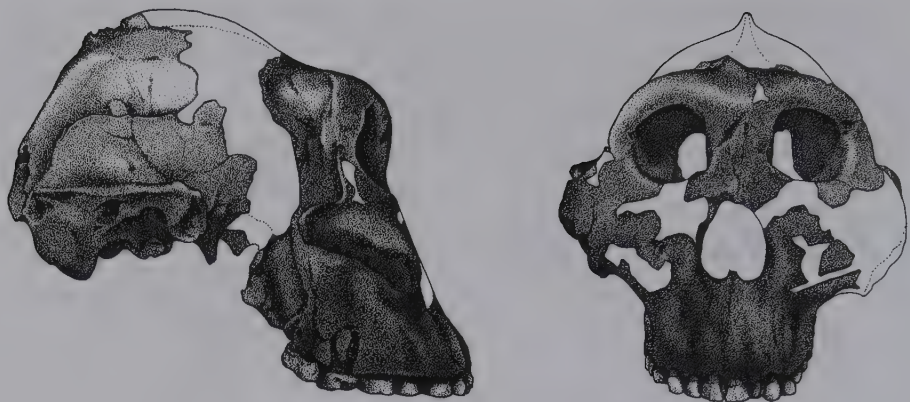
attracted comparison with the mandibles from Zhoukoudian, while many noted differences from the Mauer jaw. It was speculated on this basis that perhaps human evolution in Europe had taken a somewhat different course from that in Africa and Asia; but before opinion had a chance to crystallize on this issue, paleoanthropological attention was drawn back once more, and with a bang, to sub-Saharan Africa.

CHAPTER 8

Olduvai Gorge

While the literature of paleoanthropology was already beginning to take its modern shape in the early 1950s, the fossil record of human evolution had to await the end of that decade to follow suit. For it was essentially not until 1959 that Louis Leakey's longstanding interest in Olduvai Gorge began to pay off in the discovery of human fossils there. Following his divorce and remarriage to the archaeologist Mary Nicoll in 1936, Leakey and his new wife devoted themselves to paleontological and archaeological explorations in East Africa; but this work was conducted part-time and on a shoestring until 1948, when the American businessman Charles Boise began to fund their prospections. In 1951 this support allowed work to recommence at Olduvai, where abundant remains of various large mammals were rapidly found. In Leakey's view these were the victims of the early humans who had left behind stone tools in the same deposits. Apart from a few isolated teeth of disputed interpretation, though, there was for years no sign of these humans themselves.

Nobody who has not tried it can fully understand the amount of enthusiasm and sheer mental and physical toughness that it takes to continue searching in the broiling sun day after day, let alone year after year, for fossils that nobody can guarantee are there. Generally, you don't "dig" to find fossils, at least not in the first instance; paleontological prospection involves endless prowling or crawling across the landscape, eyes fixed on the ground for the slightest sign of bone at its surface. As fossils erode out of the enclosing sediments they are attacked by the elements and begin to fall to pieces, however complete they may have been to begin with. And complete they will rarely have been, since most fossil bones represent the remains of some ancient carnivore's dinner or have otherwise had a checkered postmortem career. The trick is thus to spot a tooth or a fractured corner of bone protruding, however slightly, from the surface rubble of the eroding deposit. Shadows, stone litter, bumps in the ground, tricks of the light, heat exhaustion, and a host of other things can throw you off. The paleontologist's dream of a landscape covered with fossil bones waiting to be picked up is usually just that, though



Side and front views of the "Zinjanthropus" cranium (OH 5) from Bed 1 of Olduvai Gorge, Tanzania. Scales are 1 cm. DM.

occasionally it has been realized. And if you are looking for a particular kind of fossil—the remains, say, of the toolmaker of Olduvai rather than of one or another of the vast numbers of large mammals which roamed the same landscape at the same time—the odds lengthen out of sight.

Zinjanthropus

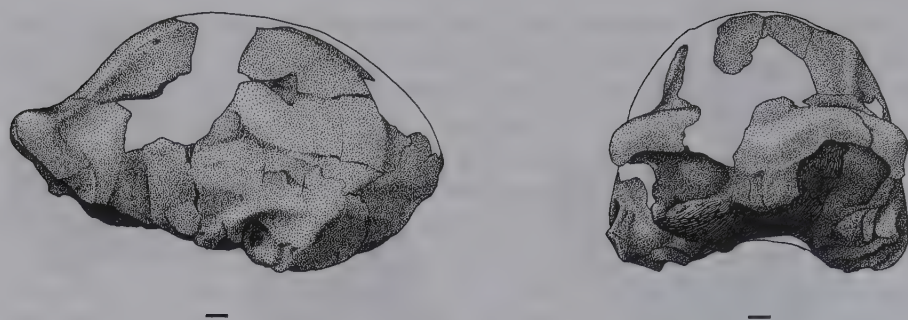
It is thus powerful testimony to the Leakeys' perseverance and optimism that in 1959 they returned yet again to Olduvai, where on a July day Mary Leakey looked once more at a site known as FLK 1. First located twenty-eight years earlier, this site, which had produced an abundance of stone tools, was believed by the Leakeys to represent a "living floor" where the toolmakers had camped and consumed the carcasses of various animals. It lay toward the bottom of Bed I and was thus early in the Olduvai stratigraphic sequence, but despite unhappy experience with his previous claims for ancient *Homo* at Olduvai, Leakey was convinced that the toolmaker of FLK, remote in time though it clearly was, must have been a member of our own genus. So convinced of this was he that in 1958 he had identified a large and rather odd-looking isolated molar tooth from higher in the section as that of a truly enormous human child "not of australopithecine type." Broom's associate John Robinson, along with others, later showed that it had belonged to an adult australopithecine. It was with some disappointment, then, that Louis received Mary's news that at FLK 1 she had spotted, eroding from the sediments, a skull whose two visible teeth appeared to be those of a robust *Australopithecus*.

Excavation of the specimen showed first impressions to be correct, however. The skull, almost complete and with a magnificently preserved set of

teeth, most closely resembled the robust specimens recovered by Broom from Swartkrans and Kromdraai, but had even more massive chewing (molar and premolar) teeth. In comparison to the huge molars, the front teeth (the incisors and canine) were tiny. The braincase was small, with a capacity of about 530 ml, but it bore a large sagittal crest, a ridge of bone along the midline of the skull produced by the attachment of powerful chewing muscles. The face was similarly unprotruding, and although it was much deeper than those of South African *Australopithecus* (a.k.a. *Paranthropus*) *robustus*, if anything known from outside South Africa was an australopithecine, this specimen was it. This created a puzzle, for even if Leakey had been pretty much alone in rejecting an australopithecine ancestry for modern humans, few were prepared to contemplate that any australopithecine had made stone tools: stone tool making, it was thought, was the hallmark of true humanity. Yet the association at FLK 1 seemed to Leakey to be unimpeachable, for the completeness of the hominid specimen contrasted with the broken-up condition of the other vertebrate bones at the site. Evidently the skull, dubbed Oldvai Hominid (OH) 5, had belonged to one of the occupants of the campsite rather than to one of their victims. In the end Leakey compromised between his earlier beliefs and his conclusion that "there is no reason...to believe that the skull represents the victim of a cannibalistic feast by some hypothetical more advanced type of man." He described his new specimen as an australopithecine, but of a new genus and species, *Zinjanthropus boisei*, which he claimed to be highly distinct from its South African relatives.

This allocation did not go unchallenged. John Robinson, for one, was quick to claim that the new specimen differed insufficiently from *Paranthropus* to be placed in a separate genus. Robinson, it should be said, was busy at the time defending the notion that a substantial ecological separation between the robust and gracile South African types mandated a generic distinction between them, this in the face of a growing consensus that all should be placed in *Australopithecus*.

Hardly was the ink dry on Robinson's riposte, than the plot began to thicken. On a tour to publicize his new find, Leakey had managed to parlay it into support from, among other agencies, the National Geographic Society, then as now a major benefactor of paleoanthropological studies. And with this new backing, work at Olduvai restarted with unprecedented vigor. At the end of 1959 full-scale excavation commenced at FLK 1 and some adjacent sites, and within a year Leakey was able to announce several more hominid discoveries. FLK I yielded a couple of lower leg bones, while at a nearby and slightly earlier locality called FLKNN 1 were found some teeth and skull fragments, some hand bones, and most of a left foot. Whether or not he thought that these fossils represented *Zinjanthropus* Leakey didn't say; but within weeks of announcing these finds he was back again in the pages of *Nature* with a new specimen from FLKNN 1 that clearly was not.



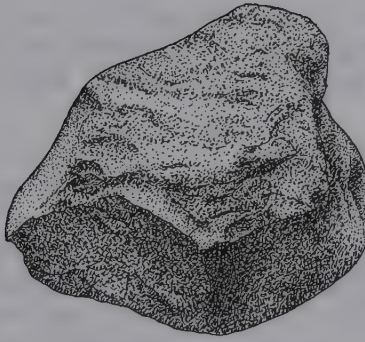
Side and front views of the Olduvai Hominid 9 skullcap from Bed II of Olduvai Gorge, Tanzania. Scales are 1 cm. DM.

“Jonny’s Child”

This specimen was the partial lower jaw of a young hominid with much smaller chewing teeth than *Zinjanthropus*, and relatively larger front teeth: an individual quite reminiscent, in fact, though Leakey was not at pains to emphasize it, of *Australopithecus africanus*. With the jaw, nicknamed “Jonny’s Child” because it was juvenile and had been discovered by the Leakey’s son Jonathan, were found bits of a braincase which appeared larger than that of OH 5; and Leakey concluded that the whole hominid assemblage from FLKNN I, skull and postcranial bones alike, belonged to a form “less specialized” than his *Zinjanthropus*. The jaw, braincase, and hand bones later acquired the number OH 7, while the foot became OH 8.

The number OH 9 went to a specimen that Leakey described at the same time but which had been found much higher in the Olduvai sequence, at the top of Bed II. This was a massive, long, and low skull vault with enormous brow ridges and a brain capacity later estimated at 1,067 ml, right in the middle of the Zhoukoudian range. Leakey didn’t commit himself as to the species identity of this “Chellean Man” specimen, so called because it was associated with a stone tool industry formerly known by that name but which we would now recognize as Acheulean; later authors—where they have bothered to render judgment—have been fairly unanimous in regarding it as an African *Homo erectus* (of which more later).

Leakey’s noncommittal description of the OH 7 jaw appeared in February of 1961. By the middle of that year he was prepared to say a little more. The specimen, he found, showed distinct differences from both *Zinjanthropus* and the South African australopithecines. These boiled down essentially to the length of the premolars, whose chewing surfaces in OH 7 were roundish in outline, rather than oval as in the australopithecines. Slender evidence on which to suggest that his “pre-*Zinjanthropus*” was not an australopithecine, but instead a “remote and truly primitive ancestor of *Homo*,” particularly since the implication was to relegate the australopithecines to a side branch of the



View of an Oldowan core tool (AMNH 95.3180) in phonolite (a volcanic rock) from Olduvai Gorge, Tanzania. Scale is 1 cm. DS.

human evolutionary tree. But this proposal did have the advantage of allowing Leakey to deny once more that the australopithecines were toolmakers. Instead, his new form became the maker of the stone tools of FLKNN I and possibly also of the more abundant ones from the *Zinjanthropus* site, FLK I.

Parenthetically, one might note that these tools were pretty unimpressive things. Termed "Oldowan" after the name Leakey had given the basal stoneworking industry of Olduvai in the 1930s, they consisted for the most part of lava or quartzite cobbles roughly shaped by a few blows with a stone hammer, sometimes while the piece was resting on another stone known as the "anvil." Mary Leakey eventually identified several distinct variants—choppers, discoids, spheroids, and so forth—and viewed all of these artifacts as "tools" with various purposes. Nowadays, in contrast, many believe that the flakes struck off these "cores" were more commonly used than the cores themselves as cutting and scraping tools, although pounding of mammal long bones to extract marrow may have been an important function of some of the larger objects. Higher in the section the basal assemblage gives way to the "Developed Oldowan" in which choppers are fewer and spheroids more numerous. "Bifaces" appear, which are cores flaked on two sides to produce a cutting edge. At this point more carefully shaped "handaxes" also begin to turn up, pointing towards the Acheulean industry associated with OH 9.

Provocative though they were, Leakey's remarkable claims for his "pre-*Zinjanthropus*" barely had time to engage the attention of his colleagues before, a week later, he dropped his next bombshell. This concerned the age of the fossils. Leakey himself had vacillated over the dating of Olduvai, but by 1959 he had returned to his original estimate that the Bed I fauna was of early Pleistocene age. No one, of course, knew at that time what the actual duration of the Pleistocene had been, though Leakey did hazard a guess in a popular

article that *Zinjanthropus* dated from about 600 kyr ago. Most felt that this figure was not unreasonable. But it was no more than a guess and was soon to be outdated by a new technique of radiometric dating: the potassium-argon (K/Ar) method.

A Dating Revolution

Like radiocarbon dating, this new approach depends on the decay of an unstable parent atom to a stable daughter product. But while radiocarbon is the prime example of the “decay” clock, based on the loss of parent atoms, K/Ar is an “accumulation” method, which measures the accretion of daughter atoms. The radioactive potassium isotope potassium-40 (^{40}K) is present as a tiny proportion of all natural potassium. Part of this decays to stable argon-40 (^{40}Ar) atoms, and if a sample of potassium-containing rock is melted in a vacuum, these atoms can be counted. The age of the sample can then be derived by comparing this amount to the known isotopic abundance of ^{40}K in natural potassium and applying the decay constant derived from its half-life. Problems may arise, however, because argon gas can get trapped mechanically in some minerals. If such argon is measured along with that derived from the decay of radioactive potassium, the resultant date will obviously be too old. It is for this reason that volcanic rocks are favorites for K/Ar dating, since they crystallize at temperatures at which no mineral can retain any argon. Any ^{40}Ar measured in uncontaminated samples of such rocks must have been derived from radioactive decay and will give a reliable estimate of how long ago the rock cooled.

Another problem for paleontologists is that fossils themselves obviously cannot be dated in this way: the method simply dates the rocks among which they are found. This is a further reason why volcanic rocks are particularly suitable for paleontological dating, because they are precise stratigraphic indicators: any volcanic event dates from a particular moment in time. Fossils are rarely found in volcanic rocks, and then almost only at the base of ashfalls; however, in a continuous sedimentary sequence fossils found in deposits just above or below a particular volcanic layer will be only slightly younger or older than that datable layer—always provided, of course, that the volcanic rock was laid down on the surface of the earth and not intruded, as lavas sometimes are, into layers already buried. Volcanic rocks derived from ashfalls do not present this problem, but even these are from time to time eroded and transported to a new site of deposition subsequent to their initial fall. Usually, however, it is possible to control for the various possible mineralogical and geological pitfalls.

At about 1.3 billion years, the half-life of ^{40}K is rather long, so ^{40}Ar accumulates rather slowly. This makes the method most suitable for dating very old rocks, though it has on occasion been used to date rocks less than 100 kyr years old. Beyond the fact that not all fossils are found in geological association

with rocks that can be dated by this method, this leaves a gap between the effective ranges of K/Ar and radiocarbon: a gap that has in recent decades been filled by a host of other methods, though each is applicable only in specific circumstances.

The K/Ar dating method was developed initially in Europe and had been used as early as 1950 for dating salt deposits some 20 million years (20 myr) old. Its use on young volcanic rocks came a decade later, however, and Olduvai was the source of some of the first such samples to be dated. Olduvai was a particularly suitable setting for such studies, because the sedimentary deposits there are interlayered with (and indeed in places largely consist of) tuffs (ashfall deposits) and lava flows. The ages of the fossiliferous sediments at the Gorge are thus bracketed by the dates of the volcanics above and below them. In July 1961 Leakey, together with the Berkeley geologists Jack Evernden and Garniss Curtis, published the first K/Ar determinations from Olduvai. The results were astonishing. A series of rock samples from tuffs low in Bed I and closely associated with the fossil localities yielded an astonishingly ancient average age of 1.75 myr. This was vastly older than anyone had imagined (though it did have the advantage of alleviating problems of the kind that had worried Leakey back in early 1960 when he contemplated the sheer implausibility of deriving modern humans from a form such as *Zinjanthropus* in what he guessed to have been a mere few hundred thousand years). And it did not go uncontested; von Koenigswald, for one, was unhappy with the 2 myr length of the Pleistocene that it implied and wrote to *Nature* saying so. But although one of von Koenigswald's coauthors was no less an authority than Wolfgang Gentner, who had produced the first ever K/Ar date over a decade earlier, the Evernden/Curtis date was rapidly accepted and has since been corroborated by many more age determinations (unsing increasingly accurate methods) from Olduvai and elsewhere.

Studies by the London anatomists John Napier and Michael Day showed that the Olduvai foot was that of a biped, but that the hand (since shown to have included a number of nonhuman elements) appeared less like that of later humans. This was uncontroversial stuff, at least at the time; indeed, everyone was treading lightly at that moment because, although there was a lot of scepticism about Leakey's claims, it seemed to most that the FLKNN I material was a little slender to argue over. In Le Gros Clark's words, it was placed in a "suspense account." Fortunately, however, material continued to accumulate from Olduvai. In 1963 a site in the lower middle part of Bed II called MNK produced a partial cranial vault and associated upper and lower jaws, which received the number OH 13. At about the same time a highly fragmentary skull and most of the teeth of a young adult hominid, dubbed OH 16, were recovered from the locality FLK II close to the bottom of Bed II. The Leakeys considered both individuals, plus a few other bits and pieces, to belong to the same kind of human as the "pre-*Zinjanthropus*" specimens from FLKNN I.



Robust mandible (NMT-W 64-160) from Peninj, Lake Natron, Tanzania. Scale is 1 cm. DM.

What they didn't find at Olduvai was a mandible to match the spectacular *Zinjanthropus* cranium. For that they had to travel some fifty miles northeast from Olduvai, to the west side of Lake Natron. In January 1964, in somewhat younger deposits now known to date from about 1.4 myr ago, they found there an almost complete lower jaw that clearly belonged to what they were now calling *Australopithecus* (*Zinjanthropus*) *boisei* (the parenthetical *Zinjanthropus* indicates a subgenus, and can pretty much be ignored since this category is close to meaningless in paleontology; from now on we'll drop the italics, though the name remains a useful convenience for informal reference).

Handy Man

Emboldened by this more substantial corpus of material, Leakey, together with his colleagues Phillip Tobias and John Napier, finally felt able to broach the question of the identity of the more lightly built human specimens from Beds I and II at Olduvai. In the *Nature* issue of April 4, 1964, they concluded that all belonged to the same species, and that this species was distinct from *Zinjanthropus* and all other australopithecines (among which, throughout this period, only John Robinson seemed really concerned to make distinctions). Reluctant to place their new form in its own genus, they opted to classify it in the genus *Homo*, as *Homo habilis* ("handy man," reflecting their belief that this was the toolmaker of lower Olduvai). Olduvai Hominid 7—the jaw,



The Olduvai Hominid 7 mandible, holotype of *Homo habilis*. Scale is 1 cm. DM.

braincase fragments, and hand bones—became the type specimen, the name-bearer of the species.

The year before, Tobias had reviewed australopithecine cranial capacities and come up with a mean size of just over 500 ml for six *A. africanus* crania; the brain of OH 7, it was estimated on the basis of the very fragmentary material available, had been somewhere around 680 ml in volume. The principal anatomical distinction between *H. habilis* and species of *Australopithecus* was thus a larger brain, and a subsidiary distinction lay in the proportions of the premolars and the anterior teeth. Of course, this move by Leakey and his colleagues involved a radical redefinition of the genus *Homo*, particularly since *Homo habilis* rather rudely violated Arthur Keith's "cerebral Rubicon" concept. And frankly the revised diagnosis of *Homo* was less than convincing, making reference, for example, to bipedalism (already present in the australopithecines) and leaning heavily on features that were either unknown in the australopithecines or which could be shown to be at the limits of variation in the latter only by lumping robust and gracile together.

Reading their description of *Homo habilis*, it is hard to avoid the conclusion that Leakey and his colleagues were swayed principally by the concept of "man the toolmaker," an ancient notion that had been gaining ground since Kenneth Oakley had published the first edition of his booklet of that name in 1949. Leakey in particular was an adherent of the idea that the unique human adaptation was the making of tools, and he was apparently prepared to subordinate anatomical considerations to cultural ones when analyzing the fossil evidence for human evolution. Of course, as we've seen, the term "human" had been deprived of any hope of precise definition as soon as it was realized that people have an evolutionary history. As long as no intermediates were believed to exist between *Homo sapiens* and its closest relatives the apes, there was no problem: people were human and apes weren't, and the keys

to humanity lay in the ensemble of those myriad perceived ways in which we see ourselves as different from apes. But as soon as it was acknowledged that modern people had acquired their uniquenesses in the course of a long process, at stages during which some of those differences had been acquired and some hadn't, the question arose (or at least appeared to arise) as to which of them was critical in defining humanity. Keith had fancied the large brain; Leakey was for tool making; today's Rubicon, as the anatomist Mike Rose pointed out, is bipedalism.

An unfortunate spinoff of this mindset was the idea of "hominization": that becoming human was in some way a definable and separate process that could be studied as such. The orthogenetic implications of this notion are clear, and it is in this guise that orthogenesis lingered longest, if in highly attenuated form, in the minds of paleoanthropologists. We'll return later to the precise ways in which this viewpoint conflicts with the actual mechanics of evolution; suffice it to say for the present that cultural associations were a powerful impetus toward the inclusion of *habilis* in *Homo*. And they took on further importance when, at a site called DK 1, low in Bed I at Olduvai, a "rough circle of loosely piled stones" was discovered that the Leakeys interpreted as a possible windbreak constructed by *Homo habilis*. Yet more cultural complexity seemed to provide an even stronger argument for regarding *habilis* as "human," irrespective of what it actually looked like.

One thing at least was certain, though: that during the lower Pleistocene a minimum of two kinds of hominid had been "evolving side by side in the Olduvai region." And perhaps elsewhere, too. Leakey and his coauthors suggested when naming their new species that Broom and Robinson's "Telanthropus" from Swartkrans, by then putatively associated with stone tools and lately transferred by Robinson to *Homo erectus*, might actually have belonged to *Homo habilis*. Further, there was soon a suggestion that two early humans might have coexisted in southeast Asia, as well. Before 1964 was out, Tobias met in Cambridge with von Koenigswald to compare the new Olduvai material with the latter's material from Java. Despite manifest differences in outlook, the two agreed to recognize four successive hominid "grades" in the lower and middle Pleistocene of Africa and Asia. The first of these was *Australopithecus* in South and East Africa and just possibly (in the form of highly fragmentary specimens from Java) in Asia. The second grade contained *Homo habilis* from Africa, and maybe also *Meganthropus palaeojavanicus*, a form that had been described by von Koenigswald on the basis of a rather robust fragment of mandible from Java. The third was represented by OH 13 from Bed II, the "Telanthropus" mandible, and a partial mandible and maxilla from Sangiran. The fourth comprised OH 9 and the Tighenif form in Africa, plus the Trinil and Zhoukoudian hominids in Asia. Thus, despite the fact that the Java specimens, in particular, remained hopelessly poorly dated, Tobias and von Koenigswald both saw distinct parallels between human evolution in Asia and Africa from a very early date.

Collegial Mutterings

All this, of course, gave Leakey's and Tobias' colleagues plenty to snipe at, especially when Leakey announced to the press that *Homo habilis* stood in the direct line to modern humans, while *Homo erectus* represented a mere side branch. The proposal of a whole new species of human, just when the juggernaut of population thinking was rolling so ponderously that almost no amount of variation was seen as too great to be contained within a single species, was generally felt to be a little much to take, even leaving aside Leakey's claims about ancestry. At and around Cambridge, where I was just beginning to learn the field at the time, there was much muttering about how there wasn't enough "morphological space" between *Australopithecus africanus* and *Homo erectus* to shoehorn in a new species. And ludicrous as it seems in retrospect—for there is indeed "space" for a battery of species between the two—this was very much in tune with the spirit of the times. At about the same moment, for instance, the American paleoanthropologist Loring Brace was launching a magnificently swingeing attack on those who would exclude the Neanderthals from the ancestry of modern humans. In an article that commanded wide attention, Brace branded as "anti-evolutionary" virtually anyone who might doubt that hominid history had been an elegantly linear progression from australopithecines through pithecanthropines to Neanderthals and thence to modern humanity. This stately (and by implication almost inevitable) process was based on Brace's perception of two consistent and overriding trends in human evolution: increasing brain size (and who could doubt the self-evident advantage of that?) and reduction of the teeth and face due, he felt, to the steady refinement of cutting tools. Brace's brash style attracted a certain degree of opprobrium, but there was widespread sympathy with his point of view, which as we'll see later became raised in certain quarters more or less to an article of faith.

Reactions to Leakey's proposals were thus colored by reluctance to complicate a picture that seemed at last to be simplifying itself. The triumph of the lumping spirit had seen the disappearance into synonymy of most of the names which had been allowed to clutter the human fossil record over the years. Proud of their newfound taxonomic sophistication, paleoanthropologists were naturally hesitant to countenance any reversal of this trend. Reactions were affected too by the common knowledge that Leakey had his own axe to grind, and had indeed been honing it for years. But there were also some more objective reasons to question the conclusions arrived at by Leakey and his coauthors, and overt discussion centered on these. The most important of them stemmed from the fragmentary nature of the Olduvai material. There was no skull of *Homo habilis*—not even a complete braincase, or a face. What's more, there was plenty of variation among the fragments known: some had relatively large chewing teeth, for example, while others had smaller ones. Perhaps most importantly, doubt was expressed about whether



Side and front views of reconstructed cranium OH 24 from Bed I of Olduvai Gorge, Tanzania. Scales are 1 cm. DM.

the *Homo habilis* type material from Bed I could justifiably be separated from gracile *Australopithecus*. And, with equal reason, it was questioned whether the Bed I and Bed II materials were properly associated in the same species. Criticism did not stop there, of course, but these particular questions are the ones it's still legitimate to ask forty years later.

The ritual prescription for alleviating the perplexity of paleoanthropologists is, of course, the discovery of more fossils. After all, it's self-evident that although the known fossil record will never be complete, the more fossils you have, the closer to completeness it will be. But the world is never quite that simple, and as usual matters were not helped by the next discovery at Olduvai. This occurred in 1968, when a badly crushed skull (OH 24) was found by Peter Nzube at DK East, a site low in Bed I and close to the famous stone circle.

The Leakeys, together with their assistant Ron Clarke, who had painstakingly restored the specimen (and was to become famous for many similar feats), found predictably enough that it belonged to the genus *Homo* as enlarged in 1964 with the addition of *habilis*. But where John Robinson had concluded that the Bed I and Bed II fossils lay in the same lineage but in different species (of *Homo*: *H. transvaalensis* and *H. sapiens*), the Leakeys still saw no reason to suppose that two different species of *Homo* had been present at Olduvai during Bed I and lower Bed II times. Moreover, in 1965 the paleoanthropologists Elwyn Simons and David Pilbeam, both then at Yale, had reviewed the Olduvai material, and had concluded that between Bed I and Bed II times dental reduction had taken place in the gracile lineage while brain size had remained rather constant. Their provisional conclusion was that the Bed I material was probably not distinct from *Australopithecus africanus*, while the Bed II specimens belonged to the same species as Robinson's *Telanthropus capensis*, potentially a member of *Homo*. But they were also prepared to entertain a variety of other possibilities, which only goes to show how much difficulty

objective observers were having in making sense of the rather scanty fossil record available during the 1960s. This record was sufficient to show that things might well have been more complicated than the nomenclatural spring cleaning in the wake of the Synthesis had suggested; but it was inadequate to support any clear-cut new picture.

It's hardly surprising, then, that it took some fifteen years and the discovery of a variety of new fossils for paleoanthropologists to become at all comfortable with the idea of *Homo habilis*. And it took longer still to see how recognizing this new species would pose as many problems as it appeared to solve. Nonetheless, it is possible in retrospect to see that, largely through the efforts of the Leakeys, the human fossil record had begun, by the mid-1960s, to take on the outline that is familiar today.

CHAPTER 9

Rama's Ape Meets the Mighty Molecule

While most members of the paleoanthropological establishment were industriously debating the significance of the Leakeys' new-found Olduvai fossils, Elwyn Simons of Yale was busy looking further back in time, toward the origin of the hominid lineage. When Simons arrived at Yale's Peabody Museum of Natural History in 1960, he inherited the curatorship of a collection of fossils made some thirty years earlier in the Siwalik Hills of northern India by G. Edward Lewis, then a Yale graduate student. Among these fossils were two jaw fragments that Lewis described in 1934 as "a much closer approximation to the Hominidae than other genera hitherto recorded," even though they were of late Miocene age (around 7–8 myr old as we now know, though they were believed in the 1960s to be about 12 myr old). He made one of them the type specimen of a new genus and species, *Ramapithecus brevirostris* (Rama's short-faced ape), named for the Hindu god. However, it was only in his doctoral dissertation (submitted in 1937) that Lewis went so far as to claim that his *Ramapithecus* partial upper jaw actually belonged to the human family—a claim he clung to in spite of a ringing denunciation in 1935 by the Smithsonian's Hrdlička, who wrote that *Ramapithecus* could not be "established as a hominid, that is, a form within the direct human ancestry." With unintended irony, though, Hrdlička also declared that it was "nearer to man than...*Australopithecus*").

A New Hominid

At least in part because his dissertation remained unpublished, Lewis' assertion languished in obscurity until 1961, when Simons ran across the *Ramapithecus* type specimen in the Peabody collections. After some thought he concluded that it was indeed hominid, and promptly described it in print as "a forerunner of Pleistocene Hominidae." A year later Louis Leakey gave the name

Kenyapithecus wickeri to a pair of maxilla fragments from 14-myr-old deposits at Fort Ternan in Kenya. At first he simply announced that his new species "exhibits a marked tendency in the direction of Hominidae," but he soon came to regard it unhesitatingly as a human ancestor. Simons agreed, and indeed in 1963 he declared (to Leakey's chagrin) that both the Kenyan and the Indian specimens belonged to a single species, by priority *Ramapithecus brevirostris*. Subsequently a variety of other teeth and bits and pieces of jaw, lower as well as upper, and from Europe and China as well as from India and Kenya, also became incorporated into *Ramapithecus*.

Given the sparse material available in the early 1960s, the argument that *Ramapithecus* was a human precursor had to rest on the shape of the teeth and palate. As in *Australopithecus* the molar teeth appeared squarish, with low crowns and rather flat chewing surfaces, while the canines and the incisor teeth (known at that time only from their empty sockets) appeared to have been much smaller than those of living apes. Moreover, the chewing teeth turned out to have quite thick enamel coatings, something not found in the African apes. No complete palate was preserved, but as reconstructed by Simons, the tooththrows of *Ramapithecus* resembled those of modern humans in describing a parabolic curve. In contrast, the tooththrows of apes form a U-shape. The divergence of its tooththrows made the palate of *Ramapithecus* appear relatively short from back to front, which in turn suggested to Simons, as to Lewis, that this hominoid had possessed a humanlike short face rather than the protruding muzzle of a modern ape.

As long as only a few suggestive fragments were known, this reconstruction was quite plausible as far as it went. But after David Pilbeam joined him as his graduate student, Simons rapidly went well beyond his early cautious statements about the ancestral human status of *Ramapithecus*. Reduction of the front teeth, wrote Pilbeam and Simons jointly in 1965, implied tool use "because smaller front teeth require the use of other means to prepare food, either animal or vegetable." What's more, "[t]he evolutionary shift in a major adaptive zone indicated in the case of *Ramapithecus* by its reduced snout and anterior teeth (premolars, canines and incisors)...may correlate with the incipient development of bipedality." In sum, "the commitment to a hominid way of life had been made by the late Miocene, and our earliest known probable ancestors...might already have adopted a way of life distinct from that of their ape contemporaries."

This was a great deal to infer from a handful of jaw fragments, but the notion that a small-brained but upright and tool-using human precursor had emerged from the pack of hominoids rather far back in time proved a seductive one indeed. For, albeit on the slender basis of a couple of features of the dentition, Pilbeam and Simons had built up a portrait of a putative human ancestor that closely reflected prevailing suppositions about how the human lineage had emerged. To take one example, an energetic debate went on more or less throughout the 1960s over the significance of canine tooth reduction

in humans. Most paleoanthropologists of the period supported Darwin's original idea, published in his *Descent of Man* in 1871, that human canines had become reduced when tools supplanted them in fighting and display. Further, they tended to believe, again with Darwin, that tools could not have been made or used if the arms and hands had been preoccupied with locomotion. Those who demurred from this orthodoxy generally affirmed the importance of tool making, but considered that this behavior should be seen simply as part of a wider cultural context; for by this time the notion of humans as essentially cultural beings had gained broad ascendancy. In this intellectual climate, it was not surprising that by the end of the 1960s it had become widely accepted among paleoanthropologists that both the genealogical and the behavioral roots of the human lineage lay back as far as 15 myr ago—and further, if you believed Louis Leakey, who by 1967 was pushing a 20-myr-old species of his *Kenyapithecus* as a human ancestor.

A Top-Heavy Edifice

As more material of *Ramapithecus* was discovered, however, this edifice proved to be top-heavy. In 1973 the paleoanthropologists Alan Walker and Peter Andrews, then both based in Nairobi, published reconstructions of the upper and lower jaws of *Ramapithecus wickeri* from Fort Ternan. New material (actually, a partial lower jaw from Fort Ternan previously identified as an ape) allowed the shape of the dental arcade to be determined with some confidence for the first time—and it proved to be of a shallow V-shape rather than the parabolic curve of Simons' reconstruction. This in itself wasn't a problem, for there were actually plenty of specimens of *Australopithecus* available to show that modern-style parabolic dental arcades weren't characteristic of those by now undoubted hominids, either. But it was symptomatic of a shift in the climate of paleontological opinion. The year before a couple of suggestions had already been published that the giant hominoid *Gigantopithecus* (another form with large, flat chewing teeth and reduced incisors and canine) might make a better candidate than *Ramapithecus* for hominid ancestry. And at around the same time other paleoanthropologists began to cast doubts more directly on the claims of *Ramapithecus* to be hominid. In 1973, for example, Christian Vogel of Germany's University of Göttingen stated flatly at a conference in Chicago that "all hitherto discussed features [of Lewis's type maxilla]...are not sufficient to warrant the inclusion of *Ramapithecus* in the Hominidae," a refrain which was later taken up by Milford Wolpoff and some of his graduate students at the University of Michigan at Ann Arbor.

Eventually, under fresh scrutiny and with new fossils available for comparison, the alleged uniquely humanlike traits of *Ramapithecus* were seen to fall away one by one, until almost the only feature that united this genus with *Australopithecus* and *Homo* was the great thickness of the enamel on the molar teeth. Then, however, it was found that the undoubted Miocene ape

Sivapithecus, which had been viewed by Pilbeam and Simons themselves as a potential ancestor of the orangutan, also shared this unusual feature. So did the orangutan, as well as *Gigantopithecus* and various other fossil apes. Finally, in 1980, Peter Andrews and his Turkish colleague Ibrahim Tekkaya delivered the paleontological coup de grace. They showed on the basis of the accumulated new fossils that the teeth of *Ramapithecus* and the ape *Sivapithecus* in fact resembled each other so closely that placing them into separate genera was not reasonable. If one of them was an ape, so was the other. And they had a new fossil, a partial face of *Sivapithecus* from Sinap, in Turkey, that showed that this beast was remarkably orangutanlike. The conclusion was clear: *Ramapithecus* was just another ape, a member of a group related to the orangutan.

By this time, Pilbeam himself had already jumped off the *Ramapithecus*-as-hominid bandwagon. On an expedition to Pakistan in 1976, a member of his field crew had found a lower jaw of *Ramapithecus* that conserved the shape of an entirely nonhumanlike dental arcade. This precipitated an influential rethinking on his part, a process that was completed during his 1979–80 field season in Pakistan with the discovery of a more or less complete 8-myr-old face and palate of *Sivapithecus*. This remarkable specimen dramatically confirmed the uncanny resemblance between the dental and facial features of *Sivapithecus* (in which genus he, too, now included *Ramapithecus*) and those of the orangutan. Pilbeam's dramatic about-face on the matter of *Ramapithecus* as a prehuman is probably the most famous and reputation-boosting case of its kind in paleoanthropology since Émile Cartailhac's legendary "Mea culpa d'un scéptique" of 1902, when the latter publicly renounced his opposition to the authenticity of the Altamira paintings. In any event, by the early 1980s *Ramapithecus* was no longer a contender for status as an early human, leaving *Australopithecus* with no obvious antecedent in the fossil record.

Enter the Molecules

By the end of the 1970s the paleontological writing was thus already on the wall for the *Ramapithecus*-as-hominid notion. But Pilbeam's change of heart, in particular, was not brought about solely by the accumulating evidence of the fossil record, nor even by the arrival of the more sophisticated ways of analyzing it that we will discuss in the next chapter. For during the 1970s an entirely new approach had been steadily penetrating into the traditionally fossil-based domain of paleoanthropology. This was molecular systematics, which actually had a respectably long pedigree, tracing its ancestry to work performed by the Cambridge University bacteriologist George Nuttall in the early years of the twentieth century. The blood constituents of different species should, Nuttall reasoned, pretty much resemble each other in proportion to the closeness of the genetic—hence phylogenetic—relationships between those species. What's more, it should be possible to determine the closeness

of those relationships by the strength of their immune systems' reaction to each other's blood proteins.

The vehicle chosen by Nuttall to investigate this idea was the "precipitin test," based on the fact that an individual's immune system will produce antibodies to fight the blood proteins of another individual as if they were invading agents of disease. If you take a sample of blood from a member of species A and inject it into a member of closely related species B, B will produce antibodies to fight the blood proteins of A. If you now take the blood serum of B (at this point known as the "antiserum" since it is full of antibodies to A) and inject it into a variety of other animals, you can see how strongly the blood of these other species reacts. The stronger the reaction, the cloudier (with "precipitin") the mixture of bloods will become. And, because closely related species share more sites on their blood molecules that can be attacked by antibodies produced to their close relative, the resulting cloudiness will increase in proportion to the similarity of the blood samples being tested. Nuttall eventually tested a very large variety of animals using these methods and found, among other things, that a closer "blood relationship" existed between humans and the large-bodied apes than between humans and the Old World monkeys, and that the New World monkeys were yet more distantly related to us. This was hardly a momentous revelation—indeed, Nuttall emphasized that this had been Darwin's own view—and there the matter rested for more than half a century, even as information continued to accumulate on the mechanisms of heredity and, ultimately, on its molecular basis.

In the early 1960s Morris Goodman of Wayne State University began to resuscitate the idea of comparing molecules, via immunological reactions, as a means of unraveling evolutionary relationships. And what he found, using techniques a lot more sophisticated than any available to Nuttall, went completely against received wisdom in anthropology. While every conventional classification of the higher primates placed humans in one family—Hominidae—and the great apes together in another—Pongidae—Goodman concluded that the African apes were so similar immunologically to humans that all should belong to the single family Hominidae. Further, while the African apes showed close immunological affinities to each other and to humans, the Asian apes, the orangutan and the gibbon, diverged from this group. Goodman then went on to bolster this argument with studies of various blood proteins using a process called electrophoresis, which sorts molecules by their size and weight. Again, he found that the African apes clustered with humans rather than with the Asian apes, supporting the idea that chimpanzees and gorillas should be classified in Hominidae along with humans, leaving the orangutan to occupy the family Pongidae in lonely state (the gibbons had long been given a family of their own). However, Goodman also found that while some molecules were most similar in humans and chimpanzees, other human blood proteins most closely resembled those of gorillas—thereby launching a debate about the exact relationships among the three that continues to this day.

Back in the early 1960s, however, Goodman's problem was getting anyone to listen to him at all. His findings went so flatly against received wisdom that traditional primate systematists rejected his findings out of hand. As an innately cautious scientist, Goodman was greatly concerned to understand just why it was that his conclusions about human-ape relationships differed so clearly from those of the morphologists (which was, in fact, partly because of inherent difficulties due to the close relationships among all the species concerned, and more importantly because a truly rational procedure for the analysis of morphology had yet to come on the scene—of which more later); and he always sought to reconcile the two lines of evidence, morphological and biochemical.

Not so Goodman's fellow biochemists Vincent Sarich and Allan Wilson, of the University of California at Berkeley. During 1966 and 1967 these researchers published a series of studies that employed a new and powerful immunological technique to compare the important blood protein known as albumin among a variety of primate species. This method, known as micro-complement fixation, provided them with a quantitative measure of albumin similarity from which they were able to construct a scheme of relationships among the species concerned.

In general, there was broad agreement between the relationships thus established and those that had been proposed by Goodman. What really upset the morphologists, however, was that Sarich and Wilson used the internal consistencies that they perceived in their data set to argue that the albumin molecule changed at a constant rate. Thus, they claimed, the "immunological distances" among species based on this molecule could be used to calculate the times that had lapsed since they had shared a common ancestor. This added insult to injury. Not only were the biochemists usurping the traditional function of the morphologists in determining relationships, but they were now moving in on the paleontologists, the guardians of the time element in evolution!

Still worse, at a time when the 14-myr-old *Ramapithecus* was still in the ascendant as a human ancestor, Sarich and Wilson's time estimates were totally at variance with this prevailing wisdom. The "molecular clock" needs to be calibrated using one date taken from the fossil record, and the date chosen by Sarich and Wilson for this purpose was one that was palatable to most paleontologists of the day: 30 myr for the last common ancestor of the apes and the Old World monkeys. The date that this yielded for the last common ancestor of humans and the African apes was not, however, palatable at all: about 5 myr. In later publications Sarich and Wilson softened this divergence date a little, but yielded nothing on principle. Indeed, in 1971 Sarich wrote, in one of the most breathtakingly provocative and undiplomatic statements in the history of human evolutionary studies, that "one no longer has the option of considering a fossil older than about eight million years as a hominid *no matter what it looks like.*"

As biochemical techniques proliferated it became clear that different methods and different molecules did not produce monolithic results: here was no magic silver bullet for systematists. Indeed, to this very day there is, among the primates, a whole variety of molecular phylogenies on offer. Most of these differ principally in detail, though in some cases there is profound disagreement; and molecular systematists argue among themselves at least as much as morphologists do. Nonetheless, it might seem surprising that back in the infancy of the debate, and in the face of united morphological opposition to molecular systematics, it was Morris Goodman who was perhaps Sarich and Wilson's most vociferous opponent. As ever trying to find some common ground between the molecular systematists and the morphologists, Goodman suggested that an extended timescale for the human family might indeed be compatible with the biochemical data. Such a reconciliation was possible if Sarich and Wilson were wrong about the constancy of molecular change, and that this had in fact slowed down among the hominoids compared to primates in general. The precise argument for such slowdown depended on the fact that hominoids have a long gestation period combined with a particularly intimate contact between the fetal and maternal blood-streams during that time. Any immunological incompatibility between the mother and the fetus over such a long period would be deeply injurious to the latter; thus, Goodman suggested, natural selection would have acted to reduce such possibilities, and hence to reduce the rate of immunological change.

But as debate between the biochemists raged, some morphologists, Pilbeam and Andrews among them, were beginning by the early 1980s to see merit in Sarich and Wilson's short phylogeny; and there's little doubt that it wasn't just new fossil evidence but also the new biochemical perspective that had speeded their reappraisal of the significance of *Ramapithecus* in human evolution. Of course, biochemistry is handicapped, even more than is the comparative anatomy of living species, in being unable to fill out the story of human evolution with the names, or the appearances, or the environments and adaptations of our various ancestors. Only the fossil record can do that. Moreover, there is no immediate prospect that useful molecular data will be extractable from higher primate fossils of any ancientness. At present, *Homo neanderthalensis* is the only extinct hominoid species in which this has been done. But from today's viewpoint Sarich and Wilson's divergence times look not too far off, and, more importantly, molecular systematics can indeed help to sort out the basic relationships among the living species that make up the group of animals to which we belong. It was certainly the use of molecular methods that led initially to the questioning of the great apes as a monolithic group distinct from ourselves, and hence gave rise to the big nomenclatural question with which we are now wrestling. Let's digress for a moment and look at this question.

What Is a Hominid?

Knowing what to call ourselves used to be simple: together with *Australopithecus* et al. we were hominids, belonging to the family Hominidae; the great apes formed the separate family Pongidae, and the gibbons another called Hylobatidae; all three families together comprised the superfamily Hominoidea. Within Hominidae there were two subfamilies: Australopithecinae for the earlier forms and a rather superfluous Homininae for members of the genus *Homo*. One sighs today for such simplicity. Now, even if one accepts that the African apes are our closest living relatives (which not everybody does; Jeffrey Schwartz of the University of Pittsburgh is a particularly persuasive advocate of the idea that the orangutan occupies that position), it is by no means clear that the three African apes (chimpanzee, bonobo, and gorilla) form a monophyletic subgroup of Hominidae (subfamily Paninae; if this were the case we would be in the subfamily Homininae) distinct from ourselves. Nobody doubts that the chimpanzees and bonobos (formerly pygmy chimpanzees) are each other's closest relatives, but neither the molecular nor the morphological approach has yet been able to sort out definitively how to resolve the human/chimpanzee-bonobo-gorilla split, although the majority money seems currently to be on the chimpanzee/bonobo group as our closest relative, at least in structural genetic terms. This uncertainty is particularly inconvenient because it leaves us in doubt whether to classify ourselves together with our fossil relatives as a distinct group at the level of the tribe Hominini or of the subtribe Homininini. And it leaves us with an equal uncertainty about how to refer to what used to be the subfamily Australopithecinae. For the rest of this book we'll continue calling these latter australopiths for the sake of convenience, while realizing that this isn't any longer quite kosher. We'll also continue using the familiar term "hominid" for the australopiths plus members of *Homo*. Certainly, if you take a "bottom-up" approach to this question of classification, there is ample justification for recognizing the full family Hominidae as thus constituted, if only on the basis of the enormous diversity of species within the group.

Of course, it's unfair to blame molecular systematics for this new classificatory dilemma, which simply results from a more accurate perception of humanity's place in nature—or, to be more precise, of the difficulties inherent in determining that place with total precision. There's no doubt in my mind that the problem would in any case soon have become apparent as a result of advances in the analysis of morphology which began to filter through into paleoanthropology in the 1970s. We'll look at those advances in another chapter; suffice it to say for the present that the fragmentary *Ramapithecus* could never have achieved distinction as humanity's remote ancestor had we known in the the 1960s what we know today about how to extract information from fossils.

CHAPTER 10

Omo and Turkana

The power of a persuasive paradigm should never be underestimated, and during the 1960s the concepts of the Evolutionary Synthesis combined with notions of culture as the basic human attribute to produce a new perspective—even dogma—on the human evolutionary process as a whole. Before that time, of course, various suggestions had been made for reducing the number of named species of early humans, but this had usually been done on a case-by-case basis. It was only during the 1960s that the notion became really popular that there *could* only ever have been one species of hominid extant at any one point in time. In formulating this concept, the advocates of the “single-species hypothesis” trawled widely for their theoretical underpinnings. From ecology they borrowed the notion that every species was defined by its ecological niche and that “competitive exclusion” would ensure that no two species could for long occupy the same niche. From Synthesis came the idea that evolution consisted exclusively of gradual change from generation to generation. And from anthropology they took the concept that humanity was defined by the possession of culture rather than by any particular physical attribute.

Hominid Catastrophism and the Single-Species Hypothesis

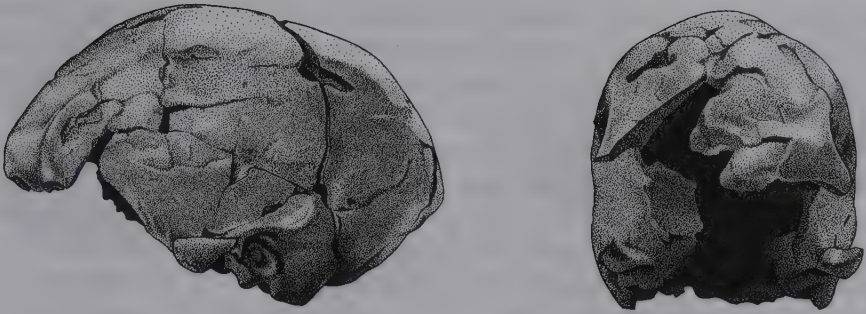
Although Theodosius Dobzhansky had trailed the single-species notion as early as 1944, it was Loring Brace who was instrumental in getting this intellectual bandwagon rolling in the mid-1960s. Generalizing to paleoanthropology as a whole the accusations of “hominid catastrophism” that he had already leveled against those who would deny ancestral human status to the Neanderthals, Brace was arguing as early as 1965 that the australopithecines (not Robinson’s *Telanthropus*) were the makers of the Swartkrans stone tools. This, he said, meant that they were culture bearing, and thus by definition belonged in *Homo*. What’s more, culture in itself constituted an ecological niche, and because of the competitive exclusion principle, no

two culture-bearing hominids could exist at the same time. The entire story of human evolution thus boiled down to a simple succession of four stages (his *Australopithecine*, *Pithecanthropine*, *Neanderthal*, and *Modern*). As parts of a continuous succession these stages could only be arbitrarily defined by breaks in the known fossil record. Specifically, he claimed that they “formed points in what was in fact a continuum.” There is indeed a certain beauty in simplicity, and here was a quite seductively simple idea that combined a variety of fashionable elements. Nonetheless, Brace’s voice went largely unheeded until Milford Wolpoff, probably the loudest voice in the business, took up the single-species cudgels.

In the years following 1967 Wolpoff proclaimed the single-species message in paper after paper and at meeting after meeting, and rapidly spawned a generation of like-minded intellectual offspring. Wolpoff deployed and elaborated all the arguments Brace had made, and quite a few besides. Among other things, he demonstrated to his own satisfaction that there was so much overlap among the various samples of South African australopithecines that they probably all belonged to the same species. There are, in fact, other reasons for this apparent overlap, but in the late 1960s not a few paleoanthropologists were prepared at least to entertain the possibility that the differences between the robust and gracile australopithecines were due to sexual dimorphism: size and shape differences between the sexes (which in the bones of modern humans, if not in those of apes, are relatively minor). And while others mumbled about how remarkable it was that all of the females had died at once at Sterkfontein, while all the males had waited around another half-million years before stampeding across the valley to become extinct at Swartkrans, it was clear that clinching evidence one way or the other was going to have to come from an expanded fossil record. Fortunately, there was not long to wait.

The Omo and Ethiopia

In 1966 the Ethiopian Emperor Haile Selassie made a state visit to Kenya. While there he met Louis Leakey, who showed him some of his fossil discoveries from Olduvai. When the Emperor inquired why there were no such things known from his own country, Leakey declared that they were undoubtedly there; it was only necessary to look for them. An invitation to do so was rapidly forthcoming. This was not in fact the first time that Leakey had contemplated fossil hunting in Ethiopia; in 1959 he had helped Clark Howell with a survey trip to the Plio-Pleistocene deposits of the Omo basin, just to the north of Ethiopia’s border with Kenya, and now Leakey called upon Howell again. And since the French paleontologist Camille Arambourg had visited the Omo some decades earlier, Leakey also invited him to participate in the Omo endeavor. In the event, for reasons of age and health, neither Leakey nor Arambourg was heavily involved with the expedition; instead, Leakey was represented by his son Richard, and Arambourg by a young French paleoanthropologist named



Side and front views of the Omo 2 braincase from the Kibish Formation, Omo Basin, Ethiopia. The more "archaic" of the two Kibish specimens. Scales are 1 cm. DM.

Yves Coppens. Richard Leakey, it should be said, had been overdosed on paleontology as a child and was at that time making his own career as a hunting guide; his father called upon him principally because of his demonstrated skill at organizing expeditions to remote places.

During the first field season, in 1967, Richard rapidly came to see that he was very much a junior partner in the enterprise, a fact that became highly evident when he was assigned the least interesting area of deposits to survey (although he did manage to recover a pair of partial human skulls, from deposits thought then to have been around 125 kyr old, which later figured importantly in discussions of the origins of anatomically modern humans). Frustrated, he borrowed a helicopter that had been hired by the expedition and flew south into Kenya, over the eastern shore of Lake Rudolf (since renamed Lake Turkana), where he had previously spotted interesting-looking sedimentary rocks. Landing, he found fossils eroding out abundantly from the sandstone: here, he decided, he would make an independent name for himself. We'll look at the historic results of this decision in a moment.

The French-American expedition continued work in the Omo until 1974, when political conditions in Ethiopia rendered further work difficult. Although this research did not result in a very bountiful harvest of hominid fossils, it was extremely important for a couple of reasons. First, abandoning the venerable Leakey-style image of the lone paleontologist, Howell insisted from the start on assembling a team of specialists—stratigraphers, geochronologists, paleoanthropologists, paleontologists of various other specialties, archaeologists, and so forth—to do the work necessary to understand the complex geology of the area and to recover and analyze the fossils recovered from it. Howell's multidisciplinary approach served as a model for all later enterprises of this kind.

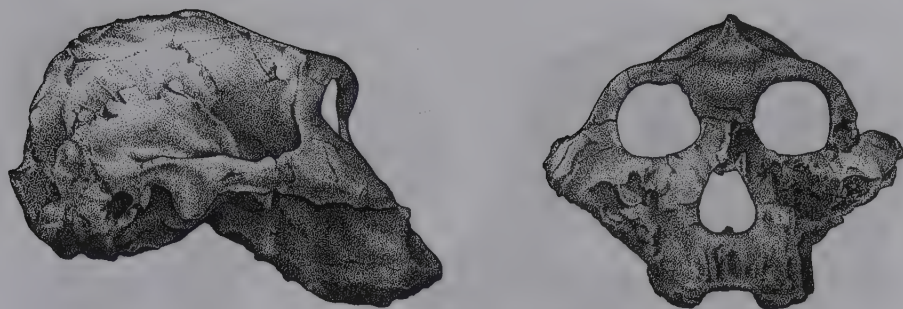
Second, the Omo deposits provide a sort of yardstick of Plio-Pleistocene history. They consist of mostly river-lain sediments of great thickness that chart the geological history of the area over almost 4 myr. Interspersed with

the fossil-containing river sediments are numerous lava flows and tuffs (layers of volcanic ashfall) that are ideal for chronometric dating. Frequent faulting made the geology extremely difficult to interpret, but it also ensured that rocks from throughout the sequence were exposed at the surface and thus collectable by paleontologists. Throughout the thick section of rock thus exposed, abundant fossil faunas were found that bore witness to the changes in animal life in the region over a long period. Howell's insistence upon exact documentation of where each fossil had come from in the section, combined with the frequency of dateable tuffs, made calibration of this sequence of biological change particularly precise. Especially useful in this endeavor were the fossil pigs, studied in detail by the paleontologist Basil Cooke. The various combinations of extinct pig species were so accurately dateable, and frequently replaced, that they could be used for dating sediments even when chronometric dates were lacking or in doubt.

Quite a few human fossils were also found in the Omo, though most of them consisted of isolated teeth because the bulk of the deposits were laid down by relatively fast-moving waters (in which prospective fossils tend to get broken or destroyed). Following the last field season, Howell analyzed these specimens and found four kinds of hominid represented. The most abundant of these was a massive robust hominid that most closely resembled Leakey's *Zinjanthropus* from Olduvai; Howell thus placed it in the species *Australopithecus boisei*. Such fossils dated to between about 2 and 1 myr ago. The oldest teeth turned up between about 3 and 2 myr ago, and were said to resemble *Australopithecus africanus* from South Africa. Later teeth (about 1.85 myr) were attributed to *Homo habilis* (helping to allay Howell's doubts about this species), and later ones yet to *Homo erectus* (about 1.1 myr). In addition to the human fossils, the team's archaeologists also found various occurrences of crude stone artifacts in deposits dating from over 2 myr ago.

Koobi Fora and the Turkana Basin

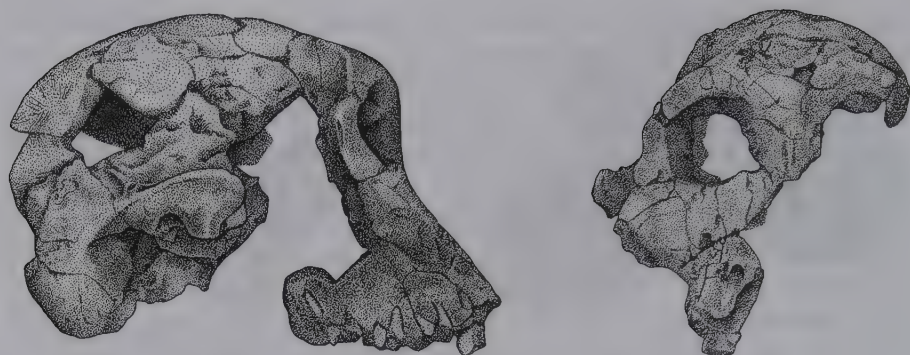
The modest hominid fossils of Omo were, however, overshadowed by the finds Richard Leakey was making along the eastern shore of Lake Turkana. Following his retreat from Ethiopia, Richard had returned to east Turkana in 1968 with a small team of specialists. This survey confirmed the great fossil potential of the area, though few fossils were actually collected at that time pending better knowledge of the local geology. This was, in fact, to prove a little ironic, since it eventually turned out that fossil locality records during the first few years of Turkana collecting were more than somewhat deficient—but we'll pick up on that story later. In any event, it was in 1969 that paydirt was really hit. That year two hominid skulls were found: one badly crushed, the other almost complete except for the teeth. The better preserved fossil, known as KNM-ER 406 (an abbreviation of its museum identification: Kenya National Museum, East Rudolf, specimen no. 406), was reminiscent of the



Side and front views of the cranium KNM-ER 406, from the KBS Member, Koobi Fora, Kenya. Scale is 1 cm. DM.

elder Leakey's *Zinjanthropus* cranium, although its face was much shallower from top to bottom, confirming the suspicion of many that OH 5 had been exceptional in this feature. It was thus allocated to the species *Australopithecus boisei*. The other cranium, ER 407, was more lightly built and was reported by Leakey as most probably belonging to a species of the genus *Homo*. Another highlight of the 1969 season was the discovery of crude stone tools within a datable tuff (the so-called KBS tuff), and Leakey felt it likely that ER 407 represented the toolmaker. The tuff itself had yielded a potassium-argon age of 2.6 myr, so already east Turkana appeared to be yielding evidence of separate *Homo* and *Australopithecus* lineages at a remarkably early date—a conclusion guaranteed to warm Louis Leakey's heart. The scene was, however, already being set for controversy: some years later ER 407 was reidentified as a female *A. boisei*. Eventually, both skulls turned out to be younger than originally thought, having come from sites that lay stratigraphically above the KBS tuff, not from below it as initially reported; and the 2.6 myr date for that tuff itself sparked a long-running argument that was eventually resolved by a reassignment to 1.9 myr.

By 1970 Leakey had assembled an impressively diversified team to work on what was now called the Koobi Fora Research Project, from the name of the site where the main camp had been established. And as the fossils began to roll in as if on a conveyor belt, each new find appeared to support Richard's initial conclusion that *Homo* and *Australopithecus* lineages had been separate at a very early date. The jewel of the 1970 season was a partial cranium (ER 732) of what everybody was to come to view as a female *A. boisei*: less massive than the male ER 406, and lacking the cranial cresting, but with much the same overall look to it. Certainly, ER 406 and ER 732 did not contrast with each other in the same way as did, say, *Australopithecus africanus* and *A. robustus* of South Africa. There were also several very large lower jaws, plus some that were much smaller but did not plausibly belong in the same species as the ER 732 cranium.



Side and front views of the cranium KNM-ER 732, from the KBS Member, Koobi Fora, Kenya. Scales are 1 cm. DM.

Here at last was more or less incontrovertible evidence that robust and gracile early hominids were not simply males and females of the same species. Yet resistance remained from two quarters: advocates of the single-species hypothesis and those who were not yet happy with the idea of *Homo habilis*. At times the two became confused; for example, straightforward opponents of *Homo habilis* occasionally trotted out the theoretical arguments for the single-species idea in support of their position. The 1971 fossil haul from Koobi Fora included some specimens that were later to assume an unexpected importance. These included the lower jaw dubbed ER 992, which came from later deposits than the fossils we've discussed so far. It also reminded many of faraway *Homo erectus*, though with well-established caution Leakey referred to it simply as *Homo* sp. (unspecified species of *Homo*). Radical rethinking thus had to await the 1972 field season at Koobi Fora, which produced the now-famous ER 1470 skull. This was found in hundreds of fragments; but painstaking reconstruction by Alan Walker revealed that much of the cranium had been preserved, although contact between the braincase and what remained of the face was minimal and the teeth were entirely gone. What was left, however, was extremely distinctive. The braincase was unexpectedly large; it had, Leakey reported, contained a brain of at least 800 ml in volume (later scaled down to about 750 ml). This contrasted with considerably under 550 ml for even the largest australopithecines and an estimated 640 ml for Louis Leakey's original *Homo habilis*. On the other hand, the face was pretty flat, and the palate was blunt and wide in a way that Leakey found reminiscent of *Australopithecus*; the chewing teeth, to judge by what was left of their roots, had been pretty large. What's more, the appearance of the specimen changed dramatically according to the angle at which the face was joined to the rest of the cranium.

All this left plenty of room for interpretation, and Alan Walker, for one, thought the specimen might as readily be assigned to *Australopithecus* as to

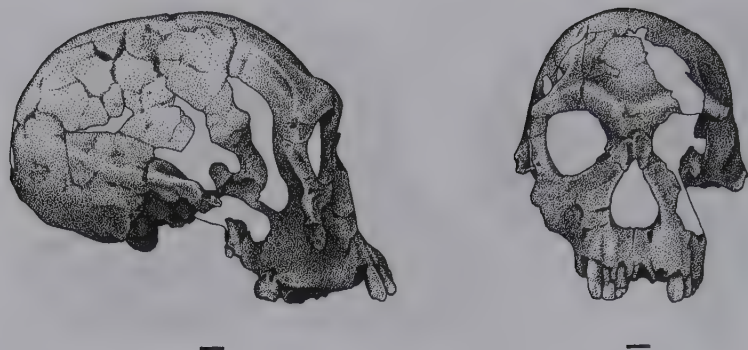


Side and front views of the cranium KNM-ER 1470, from the Burgi Member, Koobi Fora, Kenya. Scales are 1 cm. DM.

Homo. In the end, however, the brain carried the day. Leakey assigned the specimen to the genus *Homo*, but to an undetermined species. To Leakey's mind it wasn't the same thing as *Homo habilis* from Olduvai for two reasons he was prepared to admit to. Not only was the brain of ER 1470 considerably larger than that of Olduvai *Homo habilis*, but the Turkana fossil was also thought to be considerably older. From its stratigraphic position below the KBS tuff, its age was estimated at 2.6–2.9 myr. A supplementary reason for the younger Leakey's reserve may have been a natural reluctance to plunge into the acrimonious debate that still surrounded *Homo habilis*. If this was so, it's particularly ironic that ER 1470 was, rightly or wrongly, ultimately responsible for the general acknowledgement of *Homo habilis* as a valid species of early human. Still, what was pretty clear from the start was that 1470 didn't fit at all comfortably into any of the generally accepted early human species. But it equally certainly could not be ignored, and the sheer lack of definition of *Homo habilis* made it a useful slot into which this remarkable specimen could be squeezed. Suddenly, the new species had a purpose.

Meanwhile, however, new discoveries at east Turkana were muddying the waters even further. The 1973 field season turned up two more crania: ER 1805 and 1813. The first of these was both quite fragmentary and found encased in a tough matrix from which it took some time to emerge fully; and since its discovery it has been interpreted as belonging to almost every species even remotely possible. The recent consensus seems to be that its affinities lie with Olduvai *Homo habilis*. ER 1813 is a broken but quite complete cranium, with many of its teeth intact. It is quite lightly built, with a brain volume of not much more than 500 ml.

In describing it in 1974 Leakey was impressed by this cranium's resemblances to South African *Australopithecus africanus*, but others have since pointed to differences from the latter, particularly in the face. Back in 1973



Side and front views of the cranium KNM-ER 1813, from the Burgi Member, Koobi Fora, Kenya. Scales are 1 cm. DM.

most paleoanthropologists found it hard to conceive that a member of *Homo* could have had such a small brain, but eventually Clark Howell opined that 1813 might be a female *Homo habilis*, an assignment toward which most subsequent opinion has also inclined. This assignment more than anything else reflects the usefulness of having around a basket called *Homo habilis* into which paleoanthropologists could sweep a lot of fossil loose ends. And of course, the more this basket swelled, the less biological meaning it possessed—and the more welcoming it became. Richard Leakey himself was never comfortable with it and eventually grasped at the resemblances between 1813 and OH 13 from Bed II at Olduvai to argue that neither of these fossils represents *habilis* (though he thought 1470 probably did). We'll see later where this led.

As the debate over the significance of ER 1470 and the other fossils progressed, it began to be drowned out by another controversy, this time over dating. The initial dating of the KBS tuff, using a new variant of the potassium-argon method, had given it an age of about 2.6 myr, but increasingly this date seemed to be contradicted by the evidence of the faunas from Koobi Fora. In particular, as early as 1971 a brief study by Basil Cooke of pig fossils from below the KBS tuff suggested to him that they matched pigs from Omo and Olduvai which were of much younger age than the KBS was supposed to be. This later turned out to be true for various other mammals as well. Since east Turkana and Omo, at least, were not far apart, at the same point in time their faunas should have been similar; that they apparently weren't made no sense, although ingenious attempts were made to rationalize this unusual situation. A growing conflict began to emerge between Leakey's group at east Turkana and Clark Howell's contingent, still working at Omo. The Leakey side clung to the K-Ar date; the Omo group to the evidence of the fossils, calibrated by their own series of chronometric dates that suggested the KBS tuff should be about 2 myr old. This growing disagreement also brought to light the fact that the geological framework developed in the early years of fieldwork at east Turkana had been severely deficient, as had been the documentation of

exactly where each fossil had come from. Indeed, a definitive account of the geology there was not finally developed until well into the 1980s—ironically enough, led by Frank Brown, the geologist who had done so much to develop the geological framework for the Omo basin. The resulting inaccuracies in the dating of the hominid fossils naturally affected their interpretation; in particular, they enhanced Richard Leakey's claim that very early *Homo* had existed in the Turkana Basin. The argument dragged on throughout the 1970s, eventually to be resolved by a combination of new chronometric and faunal studies in favor of a date of about 1.9 myr for the KBS tuff. This made ER 1470 almost exactly contemporaneous with *Homo habilis* from Olduvai Gorge, and to most observers this increased the likelihood that they belonged to the same species. This in turn, of course, hastened the acceptance of *Homo habilis* as a real biological entity.

The Artifactual Record

A major player in the resolution of the KBS tuff dating row had been Glynn Isaac, an archaeologist who had worked with the elder Leakeys and who joined the Koobi Fora Research Project in 1970 as archaeological director. When Isaac began work in east Africa in the early 1960s, Mary Leakey was the dominant influence in the archaeology of the earliest toolmakers; after all, the crude stone tools found in the lowest levels at the Gorge were at the time by far the world's oldest known. Mary had devoted much effort to classifying the various stone artifact types she recognized in the "tool kit" of the Oldowan toolmakers, but she was also interested in the nature of the sites at which such tools were found and in what could be told from them about the activities of the early toolmakers. Some sites contained quite dense accumulations of animal bones as well as stone artifacts, and most were found in sediments that represented the margins of an ancient lake. Putting these facts together, Mary concluded that such sites were favored spots to which early hominids had brought dead animals that they butchered there with the stone tools. She thus regarded these places as "living sites," an interpretation that Isaac brought with him to east Turkana.

Turkana proved to have numerous artifact sites similar to those at Olduvai. In interpreting them, Isaac elaborated on Leakey's basic idea by introducing comparisons between the feeding behaviors of modern hunting and gathering humans and chimpanzees. Applying the ways in which humans differ from apes to sites where bones and artifacts were concentrated, he developed a model of early hominid behavior that saw these "campsites" as the focal points of a lifestyle involving the hunting and scavenging of animals (principally by males; females, encumbered by offspring, would mostly have gathered plant foods) and the transport of bits of their carcasses to a central place. Such transport was made possible by bipedal locomotion, which freed the hands for carrying. At campsites the carcasses were dismembered using

stone tools made from materials brought in for the purpose, and the food was then shared among the members of the social group. This implied complex communication among group members, which might have amounted to language, and food sharing suggested some reciprocity in social relationships. Bipedalism, language, tool making, ranging around home bases, and complex sociality involving cooperation and the division of labor between the sexes, all thus fed back into a model which saw early hominids as incipient modern humans: a model that was warmly received by most of Isaac's colleagues since it fit well with the "Man the Hunter" view of the human condition that was popular among anthropologists at the time.

Later on, though, Isaac came to change his mind about nearly all of this. As a very careful scientist, he had always been concerned about the ways in which bone and tool concentrations might have come about, and there were certainly possible explanations other than human activity for the association of tools with animal bones. Further, he eventually began to realize that perhaps it was unwise to look upon early humans as too much like ourselves. These points were being forcefully made in the late 1970s by the iconoclastic American archaeologist Lewis Binford, and eventually Isaac set in motion an intensive reexamination of the archaeological record at east Turkana. In this the first goal was to determine whether the associations between bones and tools were indeed caused by hominid activities. If they were, what precisely were those activities? And if they weren't, what processes had caused the associations? By the time of his premature death in 1985, Isaac and his collaborators had made a good start on reanalyzing these questions. Most importantly, they had shown that the best of the sites at East Turkana did indeed bear the hallmarks of early human activity. For example, cut marks on the bones at some sites showed that animals had undoubtedly been butchered there using stone tools, while half or more of the stone flakes that had been used for such cutting exhibited the kind of wear that typically results from cutting meat.

From evidence of this kind, Isaac concluded that by 2 myr ago tool-using early hominids were cutting up the carcasses of a variety of large mammals. "One can only presume," he added dryly, "that they ate the meat that they cut." Further, certain body parts were disproportionately represented at various sites, and Isaac interpreted those parts as choice cuts that had been carried in after their owners had been killed or scavenged elsewhere. So some hint of the home base idea remained, although Isaac now admitted that this did not necessarily provide evidence of behaviors such as food sharing. Indeed, he suggested replacing the idea of "food-sharing" with the more noncommittal concept of "central-place-foraging." All in all, then, the pared-down picture of the earliest tool users that remained by the mid-1980s was considerably less dramatic than that which had been drawn a decade earlier—and a lot less "human," too. But, as Isaac himself remarked, this process of simplification was necessary "to avoid...creating our origins in our own image."



Side and front views of the cranium KNM-ER 3733, from the KBS Member, Koobi Fora, Kenya. Scales are 1 cm. DM.

More from Koobi Fora

As the archaeologists were refining their methods of analysis, the paleoanthropologists were continuing to turn up new fossils at Koobi Fora. During the 1974–75 season yet another surprise came to light, in the form of a cranium dubbed ER-3733 that resembled nothing else yet known from East Turkana. In his summary in *Nature* of the season's events, Richard Leakey merely remarked upon this specimen's apparent similarity to *Homo erectus* from Zhoukoudian, but in an accompanying note coauthored with Alan Walker, he was emphatic about its assignment to this species. Provisionally, Leakey and Walker reported a cranial volume of 800–900 ml, just reaching the lower limit of *H. erectus* (the eventual determination was 848 ml.), and well above even the exceptional (though officially very much older) ER 1470. A date of between 1.3 and 1.6 myr was given for the cranium. Since such notable *Australopithecus boisei* specimens as ER 406 came from similar stratigraphic levels, Leakey and Walker took the opportunity to bash the proponents of the single-species hypothesis with the absolutely undoubted, unequivocal coexistence of two distinct hominid species at East Turkana. It may seem remarkable that at this late date it was still necessary to belabor the fact that the single-species hypothesis was totally untenable, but it did indeed take this new evidence to put it to rest for good—at least in its received form. Disappointingly, though, while Leakey and Walker sagely pointed out that a new schema for human evolution was needed, they declined to provide one of their own.

Several more hominid fossils were found at east Turkana after this, including a slightly later but more robust and quite distinctive braincase—ER 3883—that was nonetheless thought to belong to the same species as ER 3733. As the 1970s waned, though, the attention of the fossil collectors began to drift across the lake to the west Turkana region, and fieldwork in east Turkana

became focused increasingly on clarifying the geology. As we've seen, deficiencies in the early geological studies had been thrown into glaring relief by the KBS tuff dating debacle, and new blood was brought in to rectify the situation. Notable among the new arrivals was the University of Utah's Frank Brown, who had worked with Clark Howell in the Omo until research there had to be suspended. In collaboration with his graduate student Craig Feibel, now a professor at Rutgers, Brown eventually solved the problems of geological correlation between different areas of east Turkana using an ingenious new technique that allowed each of the datable tuffs in the area to be identified, wherever it was exposed, by its unique geochemical "fingerprint." The idea here is that every major eruption, even from the same volcano, emits material of slightly different—and identifiable—composition. Using these datable tuffs as markers, Brown and Feibel were able to establish a uniform geological sequence for the entire Turkana basin, into which by dint of enormous exertion they were eventually able to tie the sites of discovery of most of the fossils that had been discovered. All of the major sites fell in the time range of about 1.9–1.5 myr. Among the crania we've mentioned, the oldest were ER 1470 and 1813 at 1.9 myr; then came 407 and 1805, at about 1.85 myr; 3733 at about 1.8 myr; 406 and 732 at about 1.7 myr; and finally, 3883 at a little under 1.6 myr.

Younger than all of these was the mandible ER 992, at just over 1.5 myr. In 1975 this fossil had gained fame by being made the type specimen of the new species *Homo ergaster* ("work man") by the Australian systematist Colin Groves and his Czech colleague Vaclav Mazak. Members of the Koobi Fora Research Project were appalled by this effrontery: How could mere outsiders presume to name *their* fossil? But this is the risk you take when you describe any distinctive fossil without naming it; and if the species is indeed a distinct one, the first name given to a member of it must take precedence. And in the end many paleoanthropologists—though not Leakey or Walker—did come to the belief that *Homo ergaster* was a good species. Something similar happened in 1976, when the Russian anthropologist V. P. Alexeev made ER 1470 the type specimen of a new species that he called *Pithecanthropus* [= *Homo*] *rudolfensis*. Of all of this, more later.

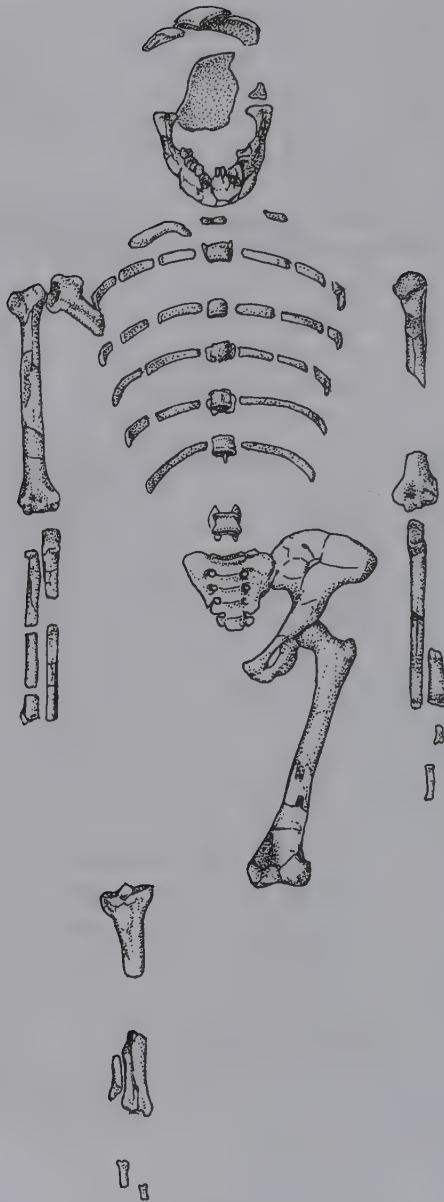
CHAPTER 11

Hadar, Lucy, and Laetoli

While Richard Leakey's discoveries in the arid badlands of east Turkana were making his name a household word, a graduate student of Clark Howell's by the name of Donald Johanson was preparing for equal fame in an equally inhospitable environment several hundred miles to the north. Johanson had accompanied Howell to Ethiopia in 1970 and 1971, and through members of the Omo expedition's French contingent he eventually met Maurice Taieb, a geologist whose field area lay in the Afar Triangle of northeastern Ethiopia. At its northern end the great East African Rift Valley splits in two, one branch heading northeast into the Gulf of Aden, and the other northwest along the Red Sea. The Afar Triangle marks the spot where the three rifting systems come together, and Taieb was studying the geological evolution of this unusual "triple junction." During his surveys in the valley of the Awash River, Taieb had noticed rocks that he thought were probably Plio-Pleistocene, and which had abundant and well-preserved fossils eroding out of them. As a specialist in plate tectonics he wasn't interested in these fossils—but maybe Johanson was? Was he! Early in 1972, he joined Taieb and Yves Coppens on a brief survey of the Afar, and at a place called Hadar they found a paleontologist's paradise: desert badlands oozing fossils that seemed, by comparison with those from Omo, to be around 3 myr. Back in Addis Ababa, Ethiopia's capital, the three agreed to launch a full-scale joint expedition, which reached the field in the fall of 1973.

Hadar, Lucy, and the First Family

That first field season at Hadar produced a remarkable find among a large haul of mammal fossils: the distal (far) end of a femur, plus the proximal (near) end of a tibia, which together made up the knee joint of a small hominoid. Short of a pelvis, perhaps, a more telling piece of the body skeleton couldn't have been found. For the knee tells you a great deal about locomotion. In a quadruped—an ape, say—the feet are held quite far apart, and each hind leg descends straight to the ground beneath the hip socket. In bipedal humans,



The skeleton of "Lucy" (NME-AL 288-1) from Hadar, Ethiopia. *DS.*

on the other hand, the feet pass close to each other during walking so that the body's center of gravity can move ahead in a straight line. If this didn't happen, the center of gravity would have to swing with each stride in a wide arc around the supporting leg—producing clumsy and inefficient movement and wasting a lot of energy. So in bipeds both femora angle inward from the hip

joint to converge at the knee; the tibiae then descend straight to the ground. In the human knee joint this adaptation shows up in the angle—known as the “carrying angle”—that is formed between the long axes of the femur and tibia. The Hadar knee joint was clearly angled; and thus it was that, at the end of the field season, it was announced at a press conference in Addis Ababa that Hadar had yielded the knee joint of a bipedal hominid that had lived between 3 and 4 myr ago.

But this was merely a foretaste of what was to come. The next year, an enlarged group of researchers at Hadar discovered, first, some hominid upper and lower jaws, and then (drumroll...) “Lucy.” Lucy, as all the world came to know in a remarkably short time, is the skeleton of a young adult female hominid, reckoned by Johanson to be some 40 percent complete. She walked upright, as numerous details of her bony anatomy confirm, but stood only a little over three feet tall. Her skull is extremely fragmentary, but it clearly had contained a brain in the ape size range (though given her diminutive stature it was probably a little bigger in comparison to body size than an ape’s). Her lower jaw is somewhat V-shaped, and while her molar teeth are quite human-like, the front premolars are not bicuspid like ours. But what was most breathtaking about Lucy was the combination of her age and her completeness. Up to 1974, the earliest reasonably complete hominid skeletons known were those of Neanderthals, much closer relatives of *Homo sapiens* and all under 100 kyr old. As documentation of earlier stages in the evolution of the hominid body, only isolated bones were available. The only pre-Neanderthal hominid specimen that came even remotely close to Lucy in completeness was Broom’s *Australopithecus africanus* pelvis from Sterkfontein, with its associated partial femur and some vertebrae. And while these remains were sufficient evidence on which to conclude that their owner had been bipedal, that was about all that could be said. Lucy, on the other hand, was complete enough to provide a pretty comprehensive picture of the kind of individual she had been. And she was also a good half-million years or more older than the fossil from Sterkfontein.

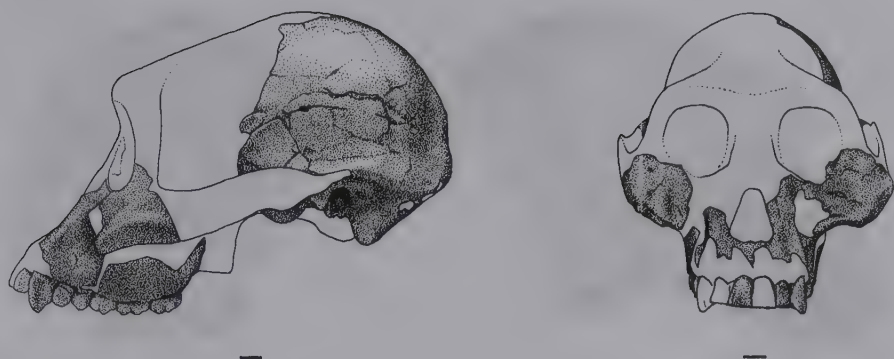
A year after the initial announcement of a 3-myr-old hominid from Hadar, then, Lucy provided clinching evidence to show that human precursors had indeed been up and walking on their hind legs at that remote point in time. But just what was Lucy? What species did she and the other Hadar fossils represent? Just before finding Lucy, Johanson had been visited in the field by Richard Leakey and other members of the Koobi Fora group. With modestly proportioned bony parts and a rather *Homo*-like balance in size between the incisor and molar teeth, the jaws that had already been found clearly did not belong to *Australopithecus boisei*, with its massive jawbones, tiny incisors, and massive chewing teeth. So Leakey, fresh from his discovery of ER 1470, quickly and predictably concluded that they must belong to an early species of *Homo*. By his own admission Johanson himself was already toying with this conclusion. On the other hand, it was clearly meaningless to consider the diminutive



Lower jaw with a complete set of teeth (NME-AL 400-1a) from Hadar, Ethiopia. Scale is 1 cm. DM.

and tiny-brained Lucy as a member of our own genus. Thus, in their preliminary description in *Nature* of the 1973 and 1974 Hadar hominids, Johanson and Taieb concluded that two or three species were represented among them: a very primitive form of *Homo* in the shape of the isolated upper and lower jaws and, in the shape of Lucy and the 1973 knee joint, something else. Just what, exactly, remained to be determined, although Johanson and Taieb felt that these remains bore comparison with *Australopithecus africanus* from South Africa. And finally, they noted resemblances to robust *Australopithecus* in a temporal bone (part of the skull wall) that was found at the end of the 1973 field season.

The undoubted if as yet obscure importance of the Hadar hominids made it imperative to get them securely dated. To help with this task Johanson, who had just been appointed to a curatorship at the Cleveland Museum of Natural History, recruited the services of James Aronson, a K/Ar dating specialist at Case Western Reserve University in the same city. Taieb had already located a datable lava flow at Hadar, plus some thin tuffs, and in 1974 Aronson visited Hadar to collect datable samples. Aronson was able more precisely to fix the position of the lava flow in the Hadar stratigraphy, and following his return to Cleveland dated it at over 3 myr, confirming preliminary dates on a sample collected earlier. Nonetheless, because of suspected weathering of the lava samples (which would have resulted in the loss of accumulated argon and thus an underestimate of the true age), it remained possible that the lava was in fact somewhat older. At the top of the section, a capping date of 2.6 myr was obtained on a tuff; this resulted in an estimated age for Lucy of about 2.9 myr, while the isolated jaws and the knee joint were older. For a variety of reasons uncertainties about the precise dating at Hadar lingered until the early 1990s, when it was found that all the many hominid fossils known by

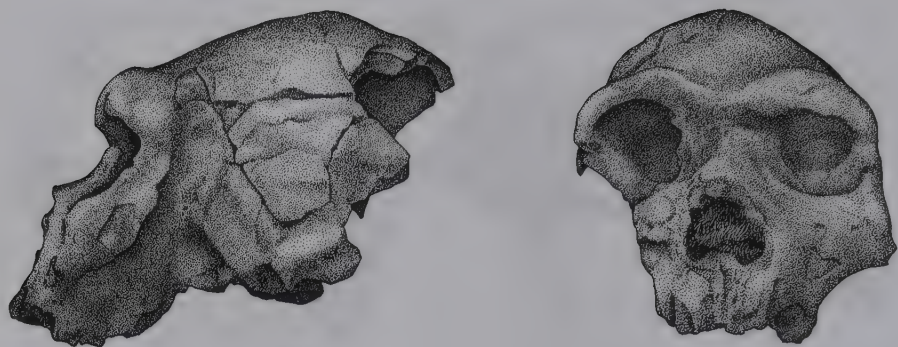


Side and front views of reconstruction of the cranium of *Australopithecus afarensis*, made from various unassociated fragments from Hadar, Ethiopia. Scales are 1 cm. DM.

then came from a rather short span of time, between about 3.2 and 3.4 myr. Lucy was the youngest among them. This made Lucy older, and the older specimens somewhat younger, than had generally been thought.

The 1975 field season saw Ethiopia in political turmoil. Haile Selassie had been overthrown in 1974, his powers assumed by a Marxist military dictatorship that took some time to take a recognizable form. Nonetheless, Johanson and his colleagues managed to get back to the Afar, and they hit the jackpot yet again. This time it was the "First Family," an unbelievable trove of some 200 early human fossils, all jumbled up next to one another in the sediments. As in the case of Lucy, nothing resembling this had ever been found before. Site 333, as the locality at which these fossils were found became designated, eventually yielded the fragmentary remains of thirteen individuals, male and female, adult and juvenile. The circumstances by which the remains of all these hominids came to be buried together in the sediments have never been definitively figured out, but one suggestion was that all may have been caught together in a flash flood. If this is the case, then it is likely that all belonged to the same social group. And although one group doesn't make much of a statistical sample, if most of its members were represented among the fossils, this would tell you something about social group size—and thirteen individuals of all ages is not out of line with expectation.

More importantly, though, if all belonged to the same social group, then all belonged to the same species. Paleontologists almost invariably have to rely on inference in determining whether different fossil individuals in fact belonged to the same species; but here, potentially, is a demonstration of this by a totally different means. Disappointingly, however, there is no unanimity on this matter of burial; some claim that the fossils accumulated sequentially over some period of time, and the debate seems set to continue, which is particularly a shame because whether or not the Hadar hominids represent a single species continues to be a particularly contentious subject in paleoanthropology.



Side and front views of the partial cranium from Bodo, Ethiopia. Scale is 1 cm. DM.

Despite continuing instability in Ethiopia, the Hadar team returned for further fieldwork in late 1976. Aside from more hominid fossils, notably many new ones from the “First Family” site, these researches resulted in the discovery by the archaeologist Hélène Roche of simple basalt tools dated at about 2.5 myr. Who had made these remarkably ancient tools remained problematic: no hominid fossils were known from this point in time, and in any case associating early stone tools with their makers has been a perennially tricky issue in paleoanthropology. Sadly, though, it proved impossible to follow up on this find. For, as the result of another military coup in Addis Ababa, the end of the 1976–77 field season marked the effective cessation of work at Hadar: work which wouldn’t resume on any major scale for well over a decade.

Bodo and Laetoli

It's probably appropriate to note here that the work at Hadar was not the only paleontology being pursued in Ethiopia during the mid-1970s. In 1976 the face of a massively built adult hominid was discovered by a team led by Johanson's rival Jon Kalb in the Middle Awash region of the Afar Depression. This specimen was found lying on sediments belonging to the Upper Bodo Beds. These contain abundant vertebrate fossils and Acheulean tools and were dated by Kalb and his associates to the Middle Pleistocene, perhaps about 400 kyr ago (with a very wide margin of error). Subsequent work has fixed the age of the Bodo cranium to about 600 myr ago. In Africa, the closest comparison of this specimen is with the famous "Rhodesian Man" cranium from Kabwe, Zambia. Judiciously enough, the Kalb team found the Bodo face to be less "archaic" than Asian *Homo erectus* or Olduvai Hominid 9, but to be more so than the Omo Kibish crania that Richard Leakey's group had discovered a few years earlier. We'll come back later to what that means; meanwhile, suffice it



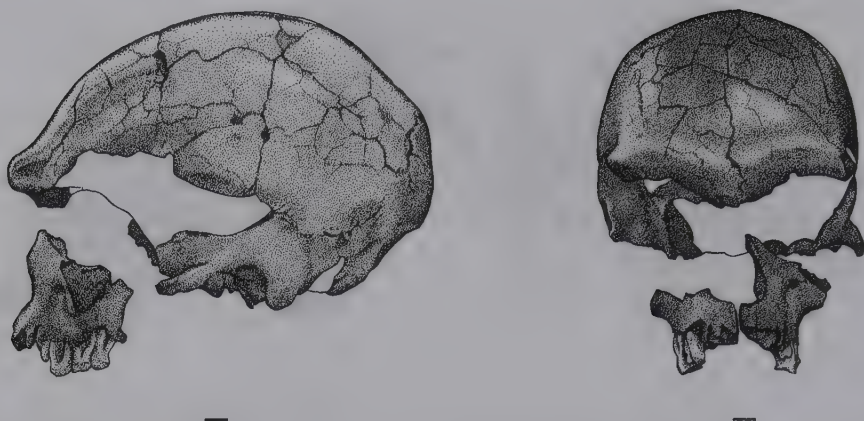
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The LH 4 mandible from the Laetoli Beds, Laetoli, Tanzania. Holotype of *Australopithecus afarensis*. Scale is 1 cm DM.

to note that during a brief survey of the same area in 1981, a group led by the veteran African archaeologist J. Desmond Clark recovered a couple of hominid fragments from very much older sediments dated at about 4 myr ago. These fossils consisted of a partial frontal bone and part of the proximal end of a femur belonging to a habitual upright biped. The frontal fragment was said by Clark and his colleagues to resemble an immature specimen known from the Tanzanian site of Laetoli, whither the focus of this story now shifts.

Laetoli, to recap, is the place about 25 miles southwest of Olduvai Gorge that was first visited by Louis and Mary Leakey in 1935. At that time they recovered an isolated lower canine tooth that Leakey thought belonged to a monkey, but which eventually turned out to have come from the jaw of an early hominid. There are several square kilometers at Laetoli over which sediments of Pliocene age are exposed, but there is much more grassy vegetation around than there is in the gorge at Olduvai. This makes it much less satisfactory from the fossil collector's point of view, so the elder Leakey rapidly turned his attentions to Olduvai, where he remained even after the German explorer Ludwig Kohl-Larsen turned up a human upper jaw fragment at Laetoli (or Garusi as he called it, for the river valley in which it lies) some four years later.

In 1950, as we've seen, Kohl-Larsen's compatriot Hans Weinert made this fragment the type specimen of the new species *Meganthropus africanus*, considering it allied to a problematic jaw fragment from Java that had been named by Franz Weidenreich in 1945. But it was not until four decades had elapsed after her first visit that Mary Leakey was to return to Laetoli to undertake prospections of any magnitude. These field researches lasted from 1974 to 1981 and yielded some thirty early hominid fossils, ranging from isolated teeth and jaw fragments to two quite well-preserved adult lower jaws: one



Side and front views of the LH 18 partial cranium from the Ngaloba Beds, Laetoli, Tanzania. Scales are 1 cm. DM.

adult (Laetoli Hominid 4) and one juvenile (LH 2). Bits of a juvenile skeleton were also recovered. Another find was of a much later and reasonably complete human skull (LH 18, known as the Ngaloba skull after the deposits in which it was found); this is somewhat archaic in appearance and has an estimated brain volume of 1200 ml. K/Ar dating on tuffs revealed that the two jaws were between 3.6 and 3.8 myr old; the Ngaloba specimen is probably in the region of 150 kyr old.

The real jewel of Laetoli, however, was a number of footprint trails preserved in very fine volcanic ash, puffed out some 3.6 myr ago by the nearby volcano Sadiman. After this powder had settled in a thin layer on the landscape, a light rain fell, turning it to something like wet cement. Before it dried out and hardened, various birds and mammals wandered over it, leaving their prints behind. Among the mammals were some early hominids, and, incredibly, at one place (Site G, excavated in 1978 and 1979) the preserved footprints of a pair of such creatures who had walked side by side were preserved over a total distance of about eighty feet. After the prints had been made and dried, the volcano erupted once more, emitting more ash that covered and protected them until they were exposed by erosion for the Leakey group to find.

This was, of course, a quite remarkable and unprecedented discovery. Most fossils provide direct evidence of bony or dental anatomy only. Any inferences about how their possessors had behaved—walked around, for instance—are just that, inferences. But here at Laetoli early human behavior itself was fossilized! Of course, these were not the only footprints of ancient humans ever to be found: others are known, for instance, from several Ice Age caves in Europe. But almost all the other fossil human footprints known are those of members of our own species, *Homo sapiens*, dating back at most a few tens of thousands of years. The Laetoli prints, in contrast, reflect the origins of the human lineage; they are the only tracks so ancient that the creatures who

made them might conceivably not have been fully bipedal—who might not have walked more or less as we do.

Of course, the world being the imperfect place it is, full agreement over the implications of the prints was long in coming—has not, indeed, been achieved yet, although nobody disputes that they are the traces left behind by upright bipeds. Similar disagreement surrounds the interpretation of the hominid fossils from Laetoli, although initially these crept quite discreetly into the literature. The jaws and teeth found at Laetoli were given for description to Tim White, a student of Milford Wolpoff's who had worked briefly at east Turkana before falling out with Richard Leakey, and who later spent the 1978 field season (when the majority of the prints were excavated) at Laetoli before falling out with Mary Leakey. In 1977, White produced a low-key and meticulous description in fine print of the Laetoli hominids discovered in 1974 and 1975 without making any comment whatever about their affinities. Descriptions of the later finds followed in 1980. I recall colleagues complaining at the time how unreadably boring these descriptions were, but—as he would shortly prove—this was hardly due to any shortage of imagination on White's part; he was simply hewing closely to a policy that the Leakeys were by then imposing on all their collaborators.

One Species or Two?

So what was this ancient biped of Laetoli, effectively the earliest hominid known? The first attempt to answer this had to await a collaboration between White and Don Johanson. Between them, these two researchers were responsible for the description of virtually all the hominid fossils known then from the period between about 4 and 3 myr ago, and it might have seemed natural that the two should have ended up collaborating on an analysis of these fossils despite the fact that they were of very different temperaments. In any event, in the summer of 1977 Johanson asked White to bring casts of the Laetoli fossils to Cleveland for comparison with those from Hadar. The obvious question was: Did the hominids from the two sites belong to the same species?

Disagreement between Johanson and White on this point was to be expected; after all, Johanson had already claimed in print that several species might be represented among the Hadar fossils, while White had trained under Milford Wolpoff, the guru of the single-species philosophy that rejected the idea that more than one hominid species could exist at any one point in time. And by Johanson's account disagreement there was, at least to start with. One problem was that there was an enormous range in size between the biggest and the smallest individuals represented among the Hadar fossils. And there were differences in morphology, too; for example, while the tiny Lucy had very diminutive front teeth (hence the rather V-shaped jaw), bigger jaws from Hadar had relatively larger front teeth. In one perspective, the size differences might simply have been the result of very substantial sexual

dimorphism within a single species, the larger fossils representing males and the smaller ones females. In that case, the shape differences would very likely have been no more than passive consequences of size discrepancies. The influence of size on shape ("allometry") had, after all, been documented long since among living organisms of all kinds. Alternatively, both size and shape differences might have been accounted for by the presence of more than one species in the sample. White favored the single-species view, despite the huge disparity in size between the largest individuals and the smallest ones. To begin with, at least, Johanson preferred the two-species interpretation he had already espoused, with the larger specimens representing some primitive species of *Homo*, and Lucy and her like something else.

The first conclusion the pair agreed upon was that all the Hadar hominids were distinct both from apes and other known hominids. Then it became evident to them that in many features a gradation in size from large to small was present within the sample, so that the question of shape differences became paramount. In the end they satisfied themselves that the shape differences were adequately accounted for by allometry, plus the differences that always occur between different individuals of the same species. At Hadar and Laetoli, between about 3.7 and 3 myr ago, they thus saw evidence of a single species of hominid that was unlike any other. This species was fully bipedal, and males were much bigger than females (somewhat as among gorillas today), though even males probably didn't stand a lot taller than four and a half feet. To judge from the pronounced muscle attachment scars on the bones, both sexes had been powerfully built. Their legs were shorter in proportion to the arms than ours are today, and their hands were like human ones in most details, though they were a bit longer and more curved. Their torsos tapered upwards. Their brains were small, in the chimpanzee range, and, again like those of apes, their faces were large and projecting. Their tooththrows converged a little toward the front, forming an arcade that was neither parabolic, as in modern humans, nor parallel-sided, as among living apes. The incisors were large, though not extraordinarily so; and while the canines were conical, as in apes, they resembled those of humans in their reduced size. The molar teeth were large and relatively flat. These distinctive hominids predated the earliest stone tools known from Hadar and almost certainly were not toolmakers.

Here, then, Johanson and White had evidence for a new species of hominid, one earlier than any other known. But a species of what genus? There were only two choices on offer: *Australopithecus* and *Homo*, and nobody who didn't wish to be hooted out of the profession would have dreamed of creating a new genus. Based more than anything else on the age of their new creature, they decided that what they had here was a stem hominid, ancestral to all subsequent human species. And if this ancestor had given rise to *Australopithecus* as well as *Homo* species, they reasoned, it couldn't itself be *Homo*. The logic of this particular proposition is not entirely clear (for if a genus located at the fork of a V can be given the name of one of the two at

the ends of the branches, it can equally well be given that of the other); but there's no doubt that given the reigning intellectual climate it was the more palatable choice. For to have called this creature a member of *Homo* would effectively have been to make our own genus equivalent to the entire expanding family Hominidae.

So the genus *Australopithecus* was selected. What was the new species to be named? Given that the fossils came from two widely separated sites, Johanson and White wanted to bind them together symbolically. This they achieved by making the Laetoli mandible LH 4 the type specimen of their new species and by calling that species *Australopithecus afarensis*, for the Afar region of Ethiopia that had yielded most of the specimens assigned to it. This, though legal, was not in fact very good procedure, for it was a good bet that someone would come along and claim that the Laetoli and Hadar materials in fact belong to different species—as has indeed happened. In the (not unlikely) event that such distinctiveness is conclusively demonstrated, the name *afarensis* will have to stay with the Tanzanian type specimen. The chosen name did, however, reflect the strength of Johanson's and White's conviction that only a single species existed at the two sites; and perhaps unexpectedly, most criticism of this idea, when it came, focused not so much on differences between the two sites as on whether more than one species might be recognized among the multitude of fossils known from Hadar.

A Stem Hominid?

The single-species idea conflicted, of course, with the views that Richard Leakey was propounding on the basis of his Koobi Fora fossils—especially given the very early date that he was still assigning to the KBS tuff. Although Leakey had never been very specific about his views on the pattern of early human evolution, his publications showed clearly that he believed, like his father, in the separation of the *Homo* and *Australopithecus* lineages from the very earliest times; to see them converging, as claimed by Johanson and White, was unpalatable to say the least. The first rumblings of trouble came in 1978, when Mary Leakey attended the meeting in Stockholm at which Johanson made the initial public announcement of *Australopithecus afarensis*. Mary had been intending to discuss the Laetoli hominids, and according to Johanson she was affronted to hear him talking about “her” specimens, even though they had been described in print and thus were in the public domain. Further, the implications of what he was saying about them were hardly congenial to her. By Johanson's account Mary had earlier agreed to join him, White, and Yves Coppens as coauthor on the publication describing the new species (with the proviso that it not suggest that any *Australopithecus* was ancestral to *Homo*; this was achieved by eliminating any discussion of the affinities of the new species). Now, however, she demanded that her name be taken off the article, something that at that stage could only be achieved by destroying the entire

print run and publishing a new version. Personal relationships between the Leakeys and the Johanson/White axis became decidedly cooler.

While all this was going on, Johanson and White prepared an interpretive paper on *A. afarensis* that laid out their ideas on the place of this species in human evolution. The article was published at the beginning of 1979 in the influential journal *Science*, and it made headlines in the popular media as well as waves in the profession. In it the pair discussed various alternative possible arrangements among the hominid species that they recognized; and they plumped for a simple forking scheme whereby the stem species *A. afarensis* gave rise, some time after 3 myr ago, to two lineages. One of these led from *Homo habilis* through *H. erectus* to *H. sapiens*; the other led from *A. africanus* to *A. robustus*, which became extinct at about 1 myr ago. They did not recognize the Leakeys' species *A. boisei* as distinct from South African *A. robustus*, and they claimed that tendencies towards the robust condition were already detectable in *A. africanus* compared to the more primitive *A. afarensis*.

This (or, to be quite frank, virtually any other) interpretation was bound to cause an outcry, and not simply from the Leakeys. One might well, indeed, have expected the response to have been even more shrill than it actually was, but it was nonetheless hardly muted. Some critics were adamant that what Johanson and White had were actually East African representatives of the species *A. africanus*, already abundantly represented from South Africa though only questionably known in eastern Africa by a few isolated teeth from Omo. Ironically—because his own new species, *Homo habilis*, had suffered the identical criticism—South Africa's Phillip Tobias was foremost among such critics. Indeed, Tobias announced during the Stockholm conference at which *A. afarensis* made its debut that the Laetoli and Sterkfontein fossils merely represented subspecies (geographical variants) of *A. africanus*. He repeated this assertion in a long paper published in 1980 in which he claimed that it was the expanded species *A. africanus* that was the progenitor of all later hominids, including the robust australopiths on the one hand and *Homo* on the other.

At about the same time Todd Olson, then of New York's City College, reviewed the same question and concluded that the bulk of the Hadar specimens and those from Laetoli in fact belonged with the robust australopithecines—which he allocated to Broom's genus *Paranthropus*. Most specifically, he found *Paranthropus* characteristics in skull base fragments from Hadar. Accepting the priority of Kohl-Larsen's species name for the Laetoli jaws and teeth (and by extension, for the larger Hadar specimens), he allocated these East African fossils to the species *Paranthropus africanus*. On the other hand, he claimed that the smallest of the Hadar specimens, notably Lucy, were indeed different. These he placed in a primitive species of the genus *Homo*, and, like John Robinson, he extended this genus to embrace the gracile South African material. Thus in Olson's view the small Ethiopian fossils, plus those traditionally placed in *Australopithecus africanus*, all belonged to the species *Homo africanus*.

Another paleoanthropologist who now saw two (or maybe more) species among the Hadar fossils was Yves Coppens, whose students Brigitte Senut and Christine Tardieu had been studying the postcranial remains. Like Olson, these researchers arrived at the conclusion that two (or maybe more) species of hominid were represented at Hadar. However, Coppens saw Lucy, along with the bulk of the material, as a member of *Australopithecus afarensis*. It was various other arm and leg bones that they saw as belonging to a primitive species of *Homo*. And Richard Leakey, of course, continued to find evidence in the sample for both *Australopithecus* and *Homo*, although he offered no detailed reasons for this perception.

The argument continues; but the Johanson/White interpretation that only a single hominid species occurred at Laetoli and Hadar quite rapidly carried the day among most paleoanthropologists, at least as a working hypothesis. Indeed, *Australopithecus afarensis* entered the accepted pantheon of ancient human precursors a good bit more rapidly than had any fossil human species previously named. But fossils are not, of course, just static objects that merely sit gathering dust in museum drawers when we are not trying to find out from them to which other fossils they are most closely related. In the final analysis they are the only witnesses we have to a long and dynamic and eventful story: a story of creatures struggling to survive and to perpetuate themselves within an environment that tends—wherever on the Earth—to be both dangerous and unpredictably changeable. And how our ancestors coped with such vagaries constitutes a significant part of the evolutionary story of our lineage.

Bipeds *and* Climbers?

At the time when *Australopithecus afarensis* was described, common wisdom ascribed the adoption of bipedalism to the need to free the hands to make tools and to carry them and other objects around. But the discovery that this upright biped was already up on its hind feet a good million years before stone tools appeared in the archaeological record obviously meant that some rethinking was called for. The most elaborate of this rethinking was done by Owen Lovejoy, of Kent State University, to whom Johanson had entrusted the description of much of the hominid postcranial material from Hadar. Lovejoy's analysis of the Lucy skeleton and other fossils convinced him that here was not only an upright biped, but a creature that was very efficiently adapted to an upright striding gait. He found, for example, that Lucy's restored pelvis not only showed all the hallmarks of our own, but additionally had more widely flaring ilia (the "blades" of the pelvis). In combination with a longer neck to the femur, this attribute improved the mechanical advantage of the muscles that stabilize the hip in the upright position. And this was possible, Lovejoy reasoned, because the small-brained *A. afarensis* simply didn't need to make the compromises that are necessary in modern humans to allow the passage through the birth canal of a large-brained newborn. He thus concluded that

in *A. afarensis* upright bipedalism was in fact more efficient than it is in ourselves.

This conclusion hasn't gone unchallenged. Their studies of the bones of the upper and lower limbs suggested to Senut and Tardieu that joint mobility was greater in *A. afarensis* than in modern humans, implying greater climbing capabilities. Bill Jungers of the State University of New York at Stony Brook pointed out that while Lucy's arms were proportionately not much longer than those of modern people, her legs were shorter, which would favor climbing. Russ Tuttle of the University of Chicago found that the length and curvature of the bones of the hands and feet suggested a strong grasping, hence climbing, capability. Henry McHenry noted high mobility in the wrist joint, which carries similar implications. Putting all this together, Jungers and his Stony Brook colleagues Randy Susman and Jack Stern concluded that whereas *A. afarensis* was undoubtedly bipedal while on the ground, it probably spent a good deal of time in the trees. They felt it likely that at night these early hominids sheltered from predators in trees, and probably also foraged there in the daytime, too.

How you look at all of this depends, of course, on which characteristics you think are most important in determining habitual behaviors. Nobody disputes that *A. afarensis* was descended at some remove from a largely tree-dwelling ancestor, although we have to bear in mind that modern great apes all spend more or less time on the ground. Obviously, terrestrial bipedalism was not acquired full-blown overnight in its full anatomical splendor, so we would expect newly bipedal hominids to show some evidence of their arboreal ancestry in their skeletal structure. And if we thus expect to find a mosaic of terrestrial and arboreal characteristics in the first habitual bipeds, which of those characteristics should we regard as most informative about behavior? Although the only plausible reason that a hominoid coming to the ground would adopt a bipedal gait there is because it was the most comfortable thing to do—because, in other words, the arboreal ancestor already habitually held its trunk upright when moving around in the trees—it is nonetheless close to certain that the newly acquired (in this case, terrestrial) features of *A. afarensis* reflect behaviors in which the species actually indulged—for why else would they have become established? So as far as the behavioral repertoire of the early terrestrial bipeds is concerned, the big question reposes on how much the ancestral tree-climbing capacity was actually used.

Australopithecus afarensis at Hadar lived in an environment that consisted of a mosaic of riverine gallery forests and more open savanna habitats, and it presumably moved through regions of both kinds (the arid grassland environment in which the Laetoli hominids left their tracks was almost certainly not typical of where they found the bulk of their sustenance). What's more, though robust, *A. afarensis* was small-bodied; and, being bipedal, it wasn't very fast. Presumably, then, this hominid was pretty vulnerable to open-country predators, and as a reasonably accomplished climber it would hardly

have refrained from using trees for shelter, particularly at night. Further, while tree-borne fruits would have been easily accessible to these creatures, as far as we know they did not make stone tools (although there is no reason to suppose that they might not have availed themselves of various soft materials, as chimpanzees do). A lack of hard tools would, however, have limited their access to many of the resources—roots, bulbs, tubers and so forth—that were potentially available on the savanna. In the deadly serious game of survival it's highly unlikely that *A. afarensis* would not have used every resource at its disposal, so on balance a behavior pattern that combined its climbing abilities with its newfound bipedal capacity seems probable. And since the anatomical structure typified by Lucy seems to have endured for several million years, this was clearly a successful behavioral strategy.

Why Bipedality?

The exact interpretation of the functional anatomy of Lucy and her kin is still disputed. It's claimed, for instance, that *A. afarensis* could not have fully extended its knee as we do, while the head (the weight-bearing portion) of the femur is much smaller than it is in ourselves, suggesting a less complete adaptation to upright posture. Nonetheless, the essentials of bipedal locomotion were undoubtedly there, and few would doubt now that bipedalism was the primordial hominid adaptation. This leads to the obvious question: Why? Owen Lovejoy thought he had the answer. In 1981 he published a paper arguing that, since the anatomically and behaviorally complex transition from ape-style quadrupedalism to upright posture could not have taken place in a single fell swoop, there must have been some countervailing advantage that increased the reproductive success of the neither-fish-nor-fowl early hominids. By themselves the females couldn't do much to increase their rate of reproduction since they were already hampered by offspring that took years to become independent. But they could achieve that result by co-opting males into the feeding of the family. Unencumbered males were better able to roam around the landscape and, if bipedal, would have had their hands free to carry food home. However, they could only benefit reproductively from such an arrangement if the offspring whose survival prospects they thereby increased were actually their own. This conveniently meshed with the females' obvious interest in having a permanent mate to depend upon. In this way Lovejoy ingeniously wove bipedalism, food carrying, and ranging around home bases into a scenario that also involved the development of pair bonding and fidelity among early hominids. In turn, through the system of permanent sexual signals that reinforced it, this bonding accounted for the marked but famously hard to explain secondary sexual differences (facial hair and prominent breasts, for instance) that distinguish human males and females.

Predictably, Lovejoy's ideas ran into a lot of criticism on a whole variety of grounds. But they had the virtue of opening up the question of the origins

of human bipedalism to an intensive reexamination. There was much discussion, for instance, of the energetics of bipedal locomotion, both in the style of humans and in that of modern great apes, all of which have a propensity for carrying their trunks upright at least under certain circumstances. Peter Rodman and Henry McHenry of the University of California at Davis, for example, showed quite elegantly in 1980 that while human bipedality is indeed inefficient compared with the quadrupedalism of a committed terrestrial mammal such as a horse, it is actually relatively efficient compared to terrestrial quadrupedalism in the ape style (which necessarily represents a compromise with locomotion in the trees). If an ape found itself having to cover long distances on the ground (as might happen as the forests in which it lived were fragmented by encroaching grassland), bipedalism might indeed be the most efficient form of locomotion for it to adopt. According to Rodman and McHenry, there was no need to invoke a fancy behavioral advantage to explain the transition from hominoid-style quadrupedalism to bipedalism, simply because it could have made good energetic sense all by itself: there was no unbridgeable energetic gulf to be crossed between hominoid quadrupedalism and hominid bipedalism.

This kind of argument fit well into a burgeoning scrutiny of the role of environmental change in the adoption of hominid bipedalism—especially after it was found that the origin of the human family probably coincided reasonably closely with a drying episode in Africa. During this drawn-out event forest cover on the continent shrank considerably and was replaced by grasslands over wide areas. The most interesting recent speculations have centered on the changed physiological demands that faced the protohominids as they began to emerge into this new environment while their ape cousins remained confined to the steadily diminishing forests. For example, the English physiologist Pete Wheeler has explained how problems of body temperature regulation, together with a shortage of drinking water, must have challenged these human precursors—and how bipedalism must have helped to meet that challenge.

Perhaps the most critical physiological problem facing any savanna-living mammal is cooling the brain, an organ that is highly sensitive to any overheating. Most savanna mammals have special mechanisms devoted to this function, but, as forest dwellers, most primates don't. The only means available to the first hominids for cooling the brain was thus to keep the whole body cool—and one way of doing this was to minimize the incoming heat load imposed by the tropical sun. This is precisely what an upright posture achieves, by reducing the area of the body exposed to the sun's direct rays. What's more, bipedalism raises the body far off the ground, where it can be cooled by the wind. In this way heat is lost by convection as well as by the evaporation of sweat—especially if the skin is not insulated by the dense hairy coat that bipedal posture makes it advantageous to shed. It is also virtually certain that early savanna-dwelling hominids would have had to range fairly widely to find food, and Wheeler calculated that at slow speeds human bipedalism demands

less energy than ape quadrupedalism. This means that less internal body heat is generated as a byproduct of energy production.

With less heat generated internally and less absorbed from the environment, and a larger proportion of the body's surface area sheltered from the sun's direct rays and thus available for radiative cooling, body temperature regulation in the tropic environment ceases to be a critical problem. Wheeler believes that the arboreal ancestors of the first human bipeds were almost certainly not committed quadrupeds; rather, they were semi-arboreal generalists which already had a propensity to hold the trunk upright. When the forests in which they had lived began to fragment and to be replaced by sun-scorched grasslands, they thus had a number of options open to them as they began to exploit the new environment; and the physiological advantages of upright posture may have been enough to tip the balance in favor of bipedal locomotion.

Later humans developed specialized means of cooling the brain, notably a "radiator" composed of tiny veins in the scalp and face. Dean Falk of Florida State University points out that this mechanism is lacking in living apes. What's more, to judge from features of the inside of the braincase that are associated with such cooling, it was also absent in the hominids from Hadar and in the robust australopithecines. Falk claims, though, that the pattern of cranial blood circulation differs in the one (juvenile) specimen from Laetoli that bears on this issue. In her view, this may place the Laetoli and Hadar fossils not simply in different species but in different lineages, the former lying on the way to gracile *Australopithecus* and *Homo*, and the latter giving rise to the robust australopithecines. This is not an interpretation that has attracted a lot of support, but it is the kind of finding that raises questions about how we interpret the fossil data at our disposal. And since the heyday of fossil hominid discoveries in Kenya and Ethiopia began in the early and middle 1970s, there have been twin revolutions in the ways in which paleoanthropologists—and paleontologists in general—view both the evolutionary process and the fossil record of evolutionary history. We'll look at those revolutions in the next chapter.

CHAPTER 12

Theory Intrudes

Quite apart from the extraordinary additions to the hominid fossil record made during the 1970s, that decade was a period of great excitement and ferment in evolutionary biology. For years paleontologists had labored mightily to fit the evidence provided by their fossils into the framework of stately change dictated by Evolutionary Synthesis; and by around 1970 some of them were coming to find that fit increasingly uncomfortable. The Synthesis, as you'll recall, elegantly explained virtually all evolutionary phenomena in terms of the gradual accretion of genetic changes in evolving lineages, under the guiding hand of natural selection. In turn this implied that species, while discrete units in space, should lose definition in the dimension of time. Species were, in fact, viewed under the Synthesis as nothing more than arbitrarily defined segments of evolving lineages which, if they didn't die out leaving no descendants, would inevitably evolve into something else. Time and anatomical change were thus thought to be more or less synonymous. The implication of this was that the fossil record should consistently show smooth intergradations from one species to the next; but, inconveniently, it too often didn't. Species, it has turned out, tend to appear rather suddenly in the fossil record, to linger for varying but often very extended periods of time, and to disappear as suddenly as they arrived, replaced by other species which might or might not be closely related to them. For a long time—indeed, since Darwin himself—this failure of the fossils to accord with expectation was explained away by the famous incompleteness of the record. But as the years passed and more and more fossils were found, the predictions of the Synthesis became increasingly out of sync with what was actually there. The time was evidently ripe for a reappraisal of paleontologists' expectations from theory—and thus of the theory itself.

Phyletic Gradualism or Punctuated Equilibria?

The doctrines of the Synthesis had not, of course, been accepted by everyone. But a concerted attack on its assumptions came only with the 1970s. The first

signs of effective opposition came in 1971, from my American Museum of Natural History colleague Niles Eldredge, who had been studying the evolution of a group of trilobites (ancient sea bottom-dwelling invertebrates) that is abundantly represented in the rocks of upper New York State and the Midwest. Eldredge had noticed that among the trilobites of interest to him there was a marked lack of evolutionary change; indeed, in the Midwest during an 8 myr span (later reduced to 6 myr) there was only one anatomical change that might be interpreted as heralding a new species. This was a decrease in the number of rows of lenses in the eye, from eighteen to seventeen: earlier sites had the eighteen-row form, later ones the seventeen-row kind. A similar pattern obtained in New York, but at one site there, which preserved a single instant in that time, fossil trilobites of both kinds were represented. And this site was very much earlier than the transition from one to the other in the Midwest. This suggested to Eldredge that a short-term speciation event (the emergence of a new species) had taken place in what is now New York, and that in the Midwest things had stayed as they were for millions of years until an environmental change had permitted the new species to invade and replace its forerunner. The message was clear: the trilobite record in this part of the United States was overwhelmingly one of stasis (stay-as-you-are) rather than of continuous change. This interpretation, which took the fossil record at its face value rather than as an inadequate reflection of the past, was of course totally at odds with the expectation of gradual change. And rather than trying to rationalize what he saw as yet another example of the legendarily incomplete record, Eldredge stuck with his idea of stasis and invoked allopatric speciation to explain the pattern he discerned.

Allopatric speciation is an old and important concept that had been most notably elaborated by Ernst Mayr to explain how one species could give rise to another. Noting that what fundamentally distinguishes members of closely related living species is their inability to produce viable and fertile offspring (an inability which, of course, paleontologists can't observe in the fossil record), Mayr had proposed that new species arise when a geographic barrier of some kind (a river, perhaps, or a mountain range, or a desert) disrupts the territory of a widespread species. The newly separated populations, formerly part of one big interbreeding whole, will then be unable to exchange genes. Since mutations and other genetic differences will continue to arise in both populations, the two will start to diverge, a process which will ultimately prevent effective reproduction between their members even if they come into contact again. In this way, two species emerge where there was only one before. Because there's less genetic inertia in the gene pools of small populations, Mayr felt it most likely that speciation and change would occur in small peripheral isolates, rather than in big chunks of the parental population. And if, by the way, you're asking just how Mayr squared this model with the grand ideas of the Synthesis that he did so much to establish, the answer is that he never quite did.

We'll look again at species, and at how they form and can be recognized by zoologists and paleontologists; suffice it for the moment to note that in geological terms allopatric speciation takes but an instant. It's also independent of long-term anatomical change. Eldredge interpreted his mixed sample of trilobites from that New York locality as a population caught in the process of allopatric speciation (for clearly this wasn't something that was taking place throughout the range of these trilobites). But Darwin and his followers had contended that the origin of species lay in adaptive modification, a slow process that took place over vast spans of time. And although the framers of the Synthesis had been careful to acknowledge that rates of evolutionary change could vary very considerably, such variations had been ascribed simply to differences in the prevailing strength of natural selection. So by regarding speciation as the basis of change, rather than as a passive result of it, and by pointing out that species tend to remain essentially unchanged over vast spans of time, Eldredge was not only totally out of tune with received wisdom, but had turned it upside down. Making a claim in the context of a specialized paper was one thing, however; getting it widely noticed was another. This Eldredge accomplished in 1972, in an article he coauthored with Harvard's Stephen Jay Gould, who had noticed the same kind of pattern in the Ice Age Bermudan land snail species he'd been studying.

The Eldredge and Gould paper was both more general and more emphatic than Eldredge's initial publication and caused an immediate stir. Perhaps its succinct and provocative title had something to do with its remarkable impact: "Punctuated Equilibria: An Alternative to Phyletic Gradualism." Starting with the proposition that preconceived frameworks affect the ways in which fossil data are viewed, Eldredge and Gould contrasted the predictions of the Synthesis with those arising from their competing theory of "Punctuated Equilibria," in which evolutionary change is seen as episodic. New species arise by the splitting of lineages, in a rapid but sporadic process whereby a single parent species gives rise to two daughter species. The history of each daughter species will be marked by an absence of steady change (although it's true that, as it spreads out, each will tend to undergo a process of geographical differentiation mediated by accommodation to differing local habitats—that will lay the basis for species differentiation in future speciation events). The upshot is that we should not expect to find steady change through time in any local rock record (for under the allopatric speciation model change will almost invariably have happened somewhere else, in a small peripheral isolate of the parent species). Further, we should at least consider the possibility that "breaks" in the fossil record, where a species suddenly disappears to be replaced by another, are real, rather than merely indicating that intermediate forms are as yet unknown. Acknowledging that their viewpoint was as likely as the traditional one of "phyletic gradualism" to color interpretation of the fossil record, Eldredge and Gould were nonetheless able to show that a

framework of punctuated equilibria more satisfactorily explained the patterns they observed in the fossil record than did the traditional model.

Finally, Eldredge and Gould posed an apparent paradox raised by their scheme. If the evolution of species is not directional, as the notion of phyletic gradualism would have it be, why do species belong to larger groups within which evolutionary trends are indeed apparent—for instance, the tendency toward a larger brain in hominid evolution? The answer to this lies in the nature of species themselves. The notion of punctuated equilibria implies that species are not simply segments of lineages that only have reality when we view them at a single instant in time. Instead, they are more like individuals, with births (at speciation) and deaths (at extinction—which can happen to species for a variety of reasons, including being outcompeted by other species which might well be their own descendants). Thus species can be seen as playing a role on the wider ecological stage that is analogous to the one played by individual organisms in pure Darwinian theory: individuals vary in their ability to survive and give rise to offspring, and so do species as they compete with each other for ecological space. The differential survival and reproduction of species therefore accounts for evolutionary trends in exactly the same way as the differential survival and reproduction of individuals does under more traditional constructs. Exactly why and how this winnowing of species occurs is still a matter of vigorous debate; but few would now question the importance of species as actors in their own right in the evolutionary play.

Reluctant Acceptance

Inevitably, the notion of punctuated equilibria ran into a good deal of opposition from some paleontologists, many of whom misunderstood the point that Eldredge and Gould were trying to make. In early days it was often said, for example, that their mechanism of evolution required saltation—the quantum leaps that the Synthesis had seen off the stage. This was, of course, quite wrong; punctuated equilibria involves speciation, not saltation, and speciation is a concept that had already been squeezed into the Synthesis by Sewall Wright, Mayr, and others. Another complaint was that Eldredge and Gould were against the idea of adaptation, and again this was untrue. Certainly, there are rather few unarguable demonstrations of adaptation (parallelism—the independent acquisition in two or more species of similar specialized anatomical features—is one of them), and fine-tuning to the environment is something that—as Eldredge pointed out—it's perhaps too easy simply to assume when we see an organism making do in its habitat. Nonetheless, adaptation is undeniably a fact of evolutionary life, and punctuated equilibria comfortably accommodates it.

It's evident that adaptation to new conditions can only take place if physical variations that are favored by those conditions arise in a population. Goodness of adaptation being entirely relative, they will tend to do this, as will less

favorable ones. New genetic and physical variants, mostly subtle, crop up in populations pretty much at random. But among widespread species the most successful of these innovations almost invariably come to be organized geographically as the species expands its range. This happens because the habitats on the periphery of the range of an expanding species are usually not typical of those in its core area, and selection will tend to favor innovations that are particularly useful under local circumstances. This is not simply a matter of theory, it's one of observation: for as I've noted, almost any widely distributed species shows distinct regional variants whose special characteristics will generally be adaptive at some level. Of course, there's room for random factors here too, especially since for reasons of statistical sampling no isolate will be entirely typical of its species as a whole. But it's uncontested that on this local level natural selection of the Darwinian kind does take place.

The implications for species change are this: when a climatic or geographic accident separates an isolate from its larger parent population, this potential new species will already differ somewhat on average from that parent; and the distinctions existing at that time will help determine the adaptive nature of the new species. The event of speciation—a multifactorial phenomenon which among mammals is very poorly understood—simply puts a permanent stamp on this divergence by establishing historical individuation, and need not itself have anything to do with adaptation as such. However, this process of geographical differentiation followed by reproductive isolation does have the effect of dramatically decreasing the size of the gene pool of the new species, and it is axiomatic in genetics that small gene pools are inherently more unstable than large ones. The new species will therefore be more susceptible to change than the parent—and this change, again, may be adaptive. It was probably such a speciation-related episode that Eldredge was witnessing in his sample of trilobites from that locality in upstate New York. If this new species is successful, as Eldredge's new trilobite evidently was, the population will expand, and the enlarged gene pool will become more resistant to change, setting the stage for anatomical stability. It's unlikely, however, that even after all this the new species will be hugely different from its parent; and of course that has implications for how we recognize species in the fossil record.

We'll come back to this; suffice it to repeat here that punctuated equilibria does indeed accommodate the notion of adaptation. And while criticism of this view of the evolutionary process didn't stop with allegations of antiadaptationism, many paleontologists did readily see punctuated equilibria as the answer to problems that they were having in the interpretation of their own fossils. The upshot is that although Eldredge and Gould unleashed a controversy in evolutionary biology that reverberates still, thirty years down the line the idea has become firmly entrenched that the short-term appearances and disappearances of entire species cannot be ignored in any comprehensive account of the history of life on Earth.

The notion of punctuated equilibria has, in fact, fit in remarkably well with a burgeoning realization of just how changeable environments have been over Earth's long biological history. For it turns out that climates and habitats have fluctuated at a pace that makes the whole idea of steady directional change over vast periods of time look rather implausible. After all, if a species finds its habitat rapidly changing, it is far more likely to migrate or to go extinct than to change on the spot; the long-term evolutionary trends that seemed so neatly to prove directional evolution have simply persisted for too long to be explained, in a see-sawing world, by gradual adaptation to steadily modifying environments, or by better adaptation to existing ones.

In any event, the advent of punctuated equilibria provided an entirely new perspective from which to view the fossil record, including that of Hominidae, and in 1975 Eldredge and I published an article in which we examined some of the implications of this perspective for paleoanthropology. We pointed out in particular that since the fossil record was by its nature a matter of discovery, so too, it had been thought, was evolutionary history. Effectively the belief was that if we crawled across enough rocky outcrops and discovered enough fossils, the history of the human lineage would eventually become revealed to us. This fit in well, of course, with the dictates of the Synthesis. For if change in lineages was gradual, then what we were out there discovering were equivalent to links in a chain, and all we had to do was to find enough of them to show how and where the chain ran. Deciphering human evolutionary history thus amounted to joining up extinct human species—conveniently defined for us by the “breaks” in the fossil record—on a timechart. But, we continued, if our evolutionary history was one of speciation, with more or less long-lived species replacing each other, what we actually had was a pattern of relationships in the fossil record: a pattern that couldn't be directly discovered, but that instead required analysis. And clearly our current methods of analysis were faulty, whatever they were; for throughout the history of paleoanthropology new discoveries, far from clarifying the picture, had tended to make it more obscure and controversial.

Reconstructing Phylogeny

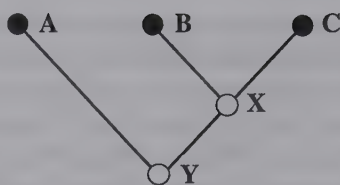
If, that is, there were traditionally any clearly articulated methods of reconstructing phylogenetic history at all. When I was a graduate student, I occupied a desk in a basement storeroom of the Peabody Museum of Natural History at Yale: one of the nation's great repositories of fossil vertebrates. As an aspiring paleontologist I was impatient to learn the arcana of the paleontologist's science. I would watch, mystified, as visiting scholars bent intently over specimens they had retrieved from collection drawers. Measurements that they took of skulls and bones seemed pretty straightforward (though I've since concluded that they are less magically informative than generally supposed). Intricate anatomical descriptions I understood, too, for anatomy lies at the heart of what

is ultimately a comparative science. But what of the other notes that these professionals so industriously made as they pored over the fossils for hour after hour? What were they doing that allowed them to penetrate the secrets of these documents of ancient life, beyond simply describing them? In those days fundamentals such as these were barely addressed at all in the average course on vertebrate evolution, where one simply served a sort of apprenticeship in learning the facts of the history of this or that group of animals, or at least the view of them favored by the professor. Eventually I plucked up the courage to ask a distinguished scholar the crucial question: How *does* one study fossils? How *does* one understand what they tell us about the history of life? The answer? "You look at them long enough, and they speak to you."

Nowadays I realize that this response has a great deal more merit than appears on the surface. Sheer intimate acquaintance with fossils, patiently acquired over long hours spent studying them, does indeed lead one to insights that go well beyond mere description and comparison. But at the time, eager as I was for a prescription telling me how to go about the conduct of the science to which I hoped to devote my career, I was frankly disappointed by this rather dusty answer. It suggested that there was no procedural Philosophers' Stone that would unlock the secret to understanding the rich tapestry of life's evolution in all of its dimensions; no trick of the trade I could learn that would admit me to the inner sanctum of paleontological professionalism. All, it seemed, depended on intuition; and how does one learn intuition? How can one be taught it?

Well, despite my disappointment at the time I'd nowadays be the last person to dispute the importance of intuition in science, for there's no doubt that it stands as the very foundation of scientific creativity. And, whatever they were, traditional methods had admittedly brought the sciences of paleontology and zoology a very long way. But they did have their limits, and as the fossil record increased by leaps and bounds their fraying edges were beginning to show. So it was a happy chance indeed that brought me in 1971 to the American Museum of Natural History in New York City, where a not-so-quiet revolution in systematics (the study of the diversity of organisms and of the relationships between them) was getting underway.

In 1950 a German entomologist named Willi Hennig published a book (in his native language) in which he articulated an approach to biological classification and the determination of evolutionary relationships that he called "phylogenetic systematics." Ernst Mayr later dubbed this approach "cladistics" (from the Greek word *clados*, meaning "branch"), because the relationships so determined were expressed in branching diagrams. Hennig's work did not attract a great deal of attention outside his homeland until 1966, when his book was translated into English. Thereafter the cladistics bandwagon began to gather momentum, as Hennig's ideas were taken up and elaborated by a group of systematists, prominent among whom were the American Museum ichthyologists Donn Rosen and Gareth Nelson. Prior to this time, most scientists had



A cladogram in its simplest form. DS.

determined relationships among organisms essentially on the basis of overall similarity between them. In paleoanthropology, for example, Wilfrid Le Gros Clark had emphasized the desirability of looking at "total morphological pattern" rather than at single characters in establishing evolutionary relationships. The problem was that it was hard for different researchers to agree on what total morphological patterns were, so that it all came down to a sort of seat-of-the-pants judgment that made competing theories of relationship hard to evaluate against each other. Hennig's great contribution was to provide a framework within which alternative hypotheses of relatedness could, in theory at least, be rigorously compared.

Forsaking the traditional representation of evolutionary relationships by lines snaking over a time chart, Hennig introduced the "cladogram," a branching diagram in which species (or larger taxa) were organized in nested sets showing their descent from a common ancestor. In the simplest case, a cladogram looks like the one shown here, which merely states that while A, B, and C are all descended from a single common ancestor, B and C share a more recent common ancestor than either does with A. How do we know this? The only way to find out is to discover one or more "derived" characters (evolutionary novelties) shared by B and C that are not present in A. These will presumably have been inherited from their hypothetical common ancestor X. Other characters shared by A, B, and C will have been inherited from Y, the common ancestor of all three, and simply show that all belong to the same group. Such characters will be derived for Y compared to its own ancestor; but as far as A, B, and C are concerned they are "primitive," i.e., common inheritances from their mutual ancestor that tell us nothing about relationships among the three. In drawing up this cladogram we do not need actually to know the ancestors X and Y as fossils; we simply infer that they existed from the distributions of characters (or, more properly, character *states*: alternative forms of the same character) among A, B, and C. What's more, neither time nor geographical distribution is a consideration in this process; we are concerned here only with morphology (which in recent times has come in this context to embrace DNA configurations as well as anatomy). Evolutionary relationships are thus determined exclusively on the basis of shared derived character state(s); and exactly the same basic process I've described here is followed in more complex cases involving more taxa.

How do we determine which character states are primitive within a group of taxa, and which are derived? At the beginning it was relatively simple. Most commonly, primitive character states are widespread within any diverse group, while derived ones have a more limited distribution. Moreover, if a character state is found in the next most closely related taxon outside the group, it can also be considered primitive, and thus of no help in determining relationships within the group. Sometimes the process of individual development can also be informative: the fact that gill slits appear early in embryonic life among humans and other land dwellers, for example, helps confirm that gills are a primitive character among vertebrates. A more controversial approach, much debated but potentially available for resolving problems for which no other solution seems to exist, is to assume that character states that first appear early in the known fossil record are more likely to be primitive than those first appearing later.

A nagging problem with the whole thing is posed by parallelism: the independent development of similar character states. Such cases obviously tell you nothing about ancestry, while obscuring the overall picture; perhaps the most striking result of the introduction of cladistic analysis was the demonstration that there is a whole lot more parallelism ("homoplasy" is the current *mot du jour* for it) around than anyone had dreamed. Actually, if you have enough characters to work with it turns out that parallelism is usually not an insuperable difficulty (a bewildering variety of computer algorithms has by now been developed that help deal with it, for instance). However, particularly if you're studying a closely knit group such as Hominidae you can never ignore it, because the more similar a pair of species is genetically, the more likely the same detailed morphology is to arise in parallel.

Whatever its difficulties, however, cladistics provides a logical procedure for the framing and testing of phylogenetic hypotheses, and it came as a breath of fresh air to one who was searching for a more satisfactory means than simple intuition of determining phylogenetic relationships. In our 1975 paper Eldredge and I included the first cladistic analysis of relationships among the hominids, and a pretty naïve effort it was, too, perhaps unsurprisingly given that it was the work of a trilobite specialist and one who had up to then been interested mainly in the lower primates. It did, however, turn up some rather surprising results. The principal one was that we found it hard to squeeze the Asian *Homo erectus* in as the intermediate between *Australopithecus* and *Homo sapiens* that it was thought to be. Various features of its long, low, flattened cranial vault, for example, are highly derived for Hominidae, but are most certainly not shared with *Homo sapiens*. What this made clear was that *Homo erectus* had been made the ancestor of *Homo sapiens* not on any compelling morphological grounds, but because it simply happened to occur at the right time to be that ancestor. And this was typical of the discoveries that early cladists were making at that time all over the vertebrate fossil record.

Unsurprisingly, perhaps, our article did not by itself make much of a splash. But it did usher cladistics into paeoanthropology, and since then this approach has steadily made inroads into our science. Some paleoanthropologists still reject cladistics, of course, appearing to equate it with some arcane form of religion; and sometimes it's hard to avoid the impression that many of those paleoanthropologists who embraced it have more deeply absorbed its jargon (which I've avoided here) than its philosophy. Nevertheless, the introduction of cladistics and the perspectives from which it stems have as profoundly affected paleoanthropology as they have the other branches of vertebrate paleontology.

Scenarios and Trees

But the rethinking of how paleoanthropologists should go about their business didn't stop with the advent of cladograms, which actually had the effect of pointing up a more general weakness of hypothesis formulation in paleontology. In 1977 Eldredge and I suggested that one of the reasons why paleoanthropology was such a contentious business was that theories of human evolution tended to be introduced at far too complex a level. If a hypothesis is to be scientific, it has to be proposed in such a way that it can at least potentially be proven wrong: it has to be objectively testable. And, as it turns out, the only kind of testable paleontological hypothesis is the cladogram, which simply tells you which taxa are most closely related to which others. It says nothing about the nature of the relationships involved. Such relationships may be of two kinds: that between an ancestor and its direct descendant, and that between two "sister" taxa descended from the same ancestor. If you add ancestry and descent (which usually also involves time) to your cladogram, you get what's called an "evolutionary tree." Johanson and White's hypothesis about *Australopithecus afarensis* was a formulation of this kind. But since it's not actually possible to *prove* ancestry (or, in some cases, to disprove it), trees are not only more complex statements than the cladogram you started with, they're also not testable. And because you can derive a number of different trees from a single cladogram, this obviously leaves the door open for endless arguments.

Yet more complex than the tree is the "scenario." This is what you get when you add the really interesting stuff to the information already present in the tree. This added information includes everything you know about adaptation, ecology, behavior, and so forth, and it's certainly what makes the past come alive. But it does mean that the average scenario is a highly complex mishmash in which considerations of relationship, ancestry, time, ecology, adaptation, and a host of other things are all inextricably intertwined and tend to feed back into each other. When you're out there selling such complicated narratives, normal scientific testability just isn't an issue: how many of your colleagues or others buy your story depends principally on how convincing or forceful a storyteller you are—and on how willing your audience

is to believe the kind of thing you are saying (which brings us back to the importance of people's expectations). Of course, this is no reason to abandon scenarios and restrict paleoanthropology to the intrinsically more limited and less interesting statements represented by cladograms and trees. But besides laying out these different levels of analysis, what Eldredge and I were at pains to emphasize was that whenever a broad interpretation of an episode of human evolution is offered, the analysis should proceed from the simple to the complex: you should start with a cladogram, advance to a clearly justified tree, and only then go on to the scenario. This way, it will be clear to everyone not only what the basic testable element is in each case, but also how the more complex hypotheses have been arrived at. Thus a basis at least will exist for discussion and comparison of those more complex hypotheses. The problem in anthropology as we saw it, and the cause of endless confusion and misunderstanding, was that people were diving in at the deep end and starting with scenarios.

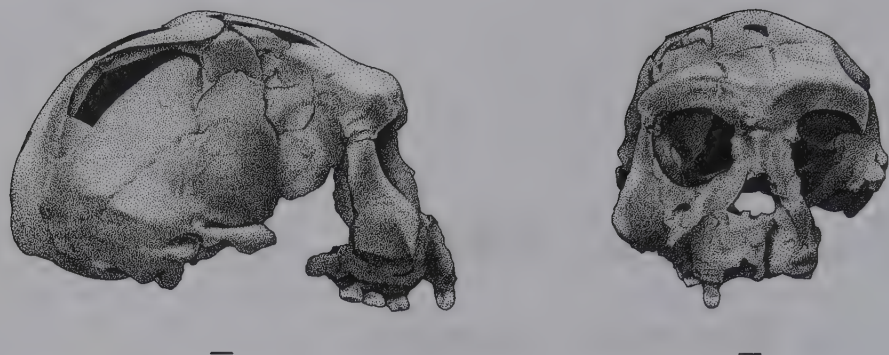
Well, old habits die hard, but progress has been made. Although some paleoanthropologists continue to burst out in hives at the mention of the word "cladistics," cladistic ways of looking at relationships have been fairly comfortably absorbed into the paleoanthropologist's wider armamentarium. Similarly, although the gradualistic view of human evolution continues to predominate in many quarters, there is an increasing awareness of the need to define and recognize accurately the species that have existed in our evolutionary past. Exactly how this should be done remains a contentious issue, which we'll look at in a later chapter; meanwhile, let's return to the fossil record itself.

CHAPTER 13

Eurasia and Africa: The Record Grows

As we've seen, during the 1960s and 1970s paleoanthropological attention was focused largely upon Africa, and upon the earlier phases of human history. But these weren't quite the only games in town. Europe and Asia were also yielding up new fossils, and new dates for old ones. On the Asian front, the most remarkable discovery of the period was a fairly complete cranium of *Homo erectus* (known as Sangiran 17), found by the Indonesian paleontologist Sastrohamidjojo Sartono in 1969. This specimen is larger than the skullcaps found before the war (its brain volume is just over 1000 ml) and considerably more robust. Its thicker brow ridges, sharper cresting across the back of the braincase, and generally heavier build suggest that—if all of these specimens belong to the same species—the new skull is that of a male while the earlier Javan skullcaps are females. Sangiran 17 is particularly interesting because it preserves much of the structure of the face, which is massively built and somewhat projecting, with huge cheekbones that flare toward the side. But it's hard to know (and is at best somewhat dubious) whether the facial structure of Sangiran 17 is a reliable guide to what the face of the Trinil or classical Sangiran specimens would have looked like; in comparable parts it is quite distinctive.

Several other more fragmentary hominid fossils were also recovered by Sartono and the paleoanthropologist Teuku Jacob at sites in central Java, and the whole known assemblage was reviewed at the end of the 1980s by Harvard's Philip Rightmire, who found no major difficulty in fitting all of the Javan hominid fossils into the species defined by Dubois's original Trinil skullcap. This was a conclusion in tune with its times; but on this, as on virtually all paleoanthropological subjects, the last word has yet to be written, and other views are beginning to be articulated. Continuing efforts to date *Homo erectus* from Java revealed substantial problems with the geology and biostratigraphy of the area; at present the best estimate is that most of the *Homo erectus* fossils from the Trinil and Sangiran localities are between about



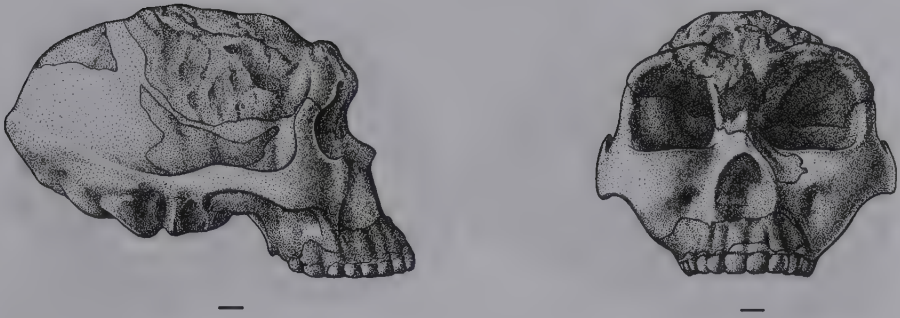
Side and front views of the Sangiran 17 skull from the Kabuh Beds, Sangiran, Java. Scales are 1 cm. DM.

1.0 myr and 700 kyr old (Trinil is at the young end), though several Sangiran specimens may be considerably older, and the Modjokerto infant cranium is claimed to be as much as 1.8 myr old. Crania from the Sambungmacan region of eastern Java may be considerably younger, perhaps only about 200 kyr old, and the Ngandong (Solo) specimens are now believed to be younger yet; but of the more recent dates and sites, more later.

The Chinese Record

Important human fossils also continued to emerge from China during the 1960s and 1970s and beyond. Zhoukoudian produced another skullcap in 1966; this proved to articulate with a cast of one of the temporal bones which was lost with the other fossils from the site in 1941, and morphologically it fits well among the prewar skullcaps. Using a combination of dating techniques, Chinese and other researchers were able to estimate a relatively late age span for the *Sinanthropus* deposits of Zhoukoudian, from about 460 to 230 kyr ago; recent rethinking may push these dates back a bit. From Lantian County of Shaanxi Province came, in 1963 and 1964, a mandible and skullcap which may be around a million years old, thus falling in the time range of the Javan remains. Despite rather poor preservation they seem to represent a broadly similar kind of hominid. Another calvaria, distinctive but of the same general form, plus some isolated teeth, came in 1980 from Hexian County, Anhui Province; this site too is poorly dated, but is probably about 400 kyr old. Two partial crania more closely comparable to those from Zhoukoudian, and dated to around 350 kyr ago, were recovered in the early 1990s from a cave site near Nanjing, in northern China.

A human cranium from China that is definitely not *Homo erectus* was found in 1978 in Dali County, Shaanxi Province. This specimen has a brain

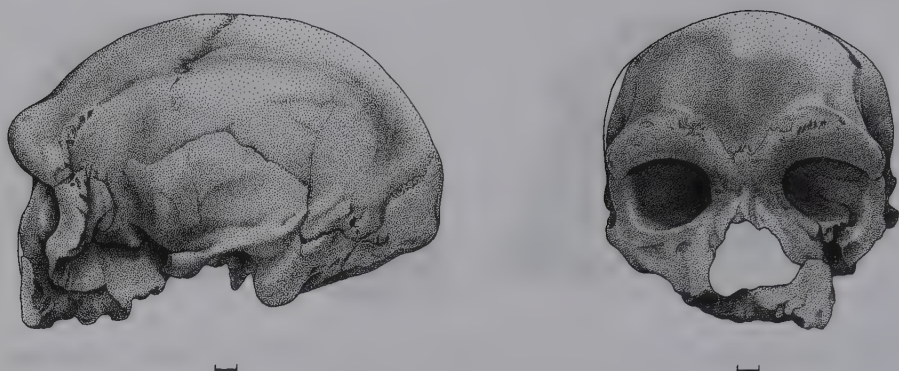


Side and front views of the reconstructed canium from Lantian, China. Scales are 1 cm. DS.

capacity of about 1,200 ml and sports a large face with tall brow ridges. It is uncertainly dated but is probably around 200 kyr old.

Although adequate description of the Dali cranium is slow in seeing the light of day, this specimen seems to fit among the "intermediate" group, also exemplified by the crania from Kabwe and Bodo in Africa, which lies at least in time between most *Homo erectus* and *Homo sapiens*. This is reflected in the way in which it has been classified by Chinese investigators: it was initially described by Yuan Wang and his collaborators as *Homo erectus*, while later Wu Xinzhi of the Institute of Vertebrate Paleontology and Paleoanthropology in Beijing placed it in a separate subspecies of our own species, as *Homo sapiens daliensis*. However, if we think in terms of morphology instead of time, it makes more sense to classify it, along with the African crania and the European specimens from Petralona and Arago about to be described, in the apparently cosmopolitan species *Homo heidelbergensis*. A closely similar morphology is seen in the cranium associated with a more recently discovered (1984) Chinese partial skeleton from the site of Jinniushan, in Liaoning Province, which appears to be broadly comparable in age.

About the same age, too, is a skullcap found in 1958 at Maba, Guangdong Province, which is lightly built but has a brow ridge with a rather arching contour that, remarkably, calls to mind what is seen in Neanderthals. Despite its distinctive and currently enigmatic morphology, this specimen has generally been regarded in China as an early *Homo sapiens* cranium that bears affinities to modern Asians, while retaining some features of *Homo erectus*. A similar claim has also been made for a couple of badly crushed crania, maybe about 400 kyr old, that were found in 1989–90 at Yunxian, in Hubei Province. Poorly preserved as they are, it is worth noting that one of them has a supra-orbital structure that appears reminiscent of *Homo heidelbergensis*. Whatever the affinities of these various Chinese specimens may ultimately turn out to be, it is clear that in eastern Asia, as elsewhere in the Old World, the hominid fossils are giving us a clear signal of diversity rather than of linearity.

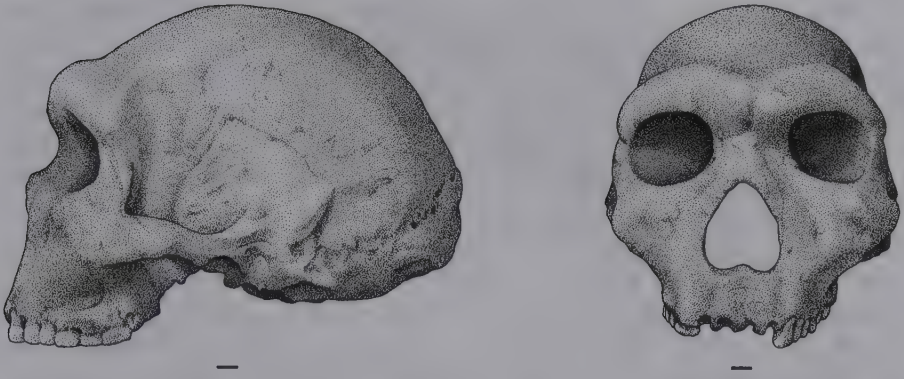


Side and front views of the damaged and distorted cranium from Dali, China. Scales are 1 cm. DM.

Homo heidelbergensis

Still, the ways in which the Chinese specimens have been interpreted by their describers reflect the long-prevailing wisdom that any Middle Pleistocene fossil human must belong either to *Homo sapiens* or to *Homo erectus*. This is a mindset that has proven very hard to shake, and it is one that has afflicted European paleoanthropologists quite as much as it has done their Chinese counterparts. In 1960, for example, a cranium was found in a cave at Petralona, in north-eastern Greece. This is a marvelously preserved specimen that has only fairly recently been totally cleaned of the calcite coating that had covered and protected it. Unfortunately, the calcite matrix that was removed was not kept, for it might have been used for dating using a new technique that I'll explain later; as it is, the specimen has been claimed to be as much as 700 kyr old, although the latest sifting of the rather confusing evidence by the geochronologist Rainer Grün puts it much more plausibly in the 250–150 kyr range. The Petralona fossil itself is clearly neither *Homo erectus* nor *Homo sapiens* (though it has been claimed to be both): it had a relatively large brain of about 1,200 ml in volume, but the skull vault, while better inflated than that of *Homo erectus*, is longish, with a clearly retreating forehead behind large brow ridges, and is clearly angled at the back. The face is large and projects distinctly, especially in the midline. Although early reports described this specimen as belonging variously to *Homo erectus* and *Homo sapiens*, most opinion veered quite quickly toward an "archaic" form of the latter, clearly distinct from both modern humans and Neanderthals. Recent studies have detected some Neanderthal-like features in its face, but, if there, these are subtle indeed; and particularly in the conformation of the tall and "twisting" supraorbital (eyebrow) region this specimen does not resemble Neanderthals at all.

What it does resemble in this part of the cranium is a fossilized facial skeleton that was excavated, along with a variety of other hominid fossils, by Henry de Lumley and his colleagues at the cave of Arago in the foothills of



Side and front views of the cranium from Petralona, northern Greece. Scales are 1 cm. DM.

the French Pyrenees, close to Perpignan and the Spanish border. From 1964 onwards work at this remarkable site revealed a stratified succession of living floors, with an abundance of animal bones and rather crude stone tools (mostly flakes of one kind or another; rather few handaxes). The age of the deposits has proven difficult to determine, but most would now reckon that the human fossils are about 400 kyr old, give or take 100 kyr or so. Among the first of them to show up were a couple of partial lower jaws that are both robust and lack chins, but which differ noticeably in size. This difference is generally ascribed to sexual dimorphism. The most interesting specimen, found in 1971, is the well-preserved if somewhat distorted face just mentioned, together with an apparently associated parietal bone. These two elements have been used to produce a reconstruction of the cranium, which has an estimated volume of 1,100–1,200 ml. Overall, the reconstructed skull is generally quite Petralonalike, with a modestly inflated cranial vault that recedes behind tall brow ridges with a flattish anterior surface that “twists” up and back toward the sides. The face projects modestly and is rather lightly built; this has caused some to suggest that the cranium is that of a female, although its describers preferred a male designation. In early days the Arago hominid was often described for convenience as a “pre-Neanderthal,” more for reasons of dating than of morphology; recent studies have actually detected some Neanderthal-like traits, particularly in the lower jaw. The closest cranial comparison, however, is clearly with Petralona in Europe, and with the more robust Kabwe and Bodo specimens in Africa; the best match for the lower jaws lies in Otto Schoetensack’s Mauer mandible, the type specimen of *Homo heidelbergensis*.

The de Lumley group backed the allocation of the Arago hominids to an “advanced form” of *Homo erectus*, and until fairly recently this usage was generally followed by continental European paleoanthropologists (because clearly these and similar fossils are not *Homo sapiens*). English-speaking scientists, on

the other hand, mostly preferred to regard them as belonging to “archaic *Homo sapiens*” (because, equally clearly, they are not *Homo erectus*). Here we have a perfect example of how expectation has colored interpretation of the fossil record. Because received wisdom tells us that *Homo erectus* evolved gradually into *Homo sapiens* (and because it admits no named intermediate stages), we should expect to find forms that might be classified either way. And since Arago and its like are at least roughly intermediate between these species both in time and, at least as importantly, in brain size (an attribute which appeals powerfully both because it is so easy to quantify and because it somehow expresses the essence of humanness), we not only expect to find them by their nature impossible to classify, but we don’t bother to examine their morphology very closely. If we did, however, we might reach a very different conclusion about their relationships, and we might particularly bear in mind the resemblances between the Arago mandibles and the Mauer holotype of *Homo heidelbergensis*.

To sum up, then, there was a lot of very vocal and ultimately fruitless discussion of these various new finds from Asia and Europe. But aside from eliciting differences of opinion on what to call them, they initially did rather little to stimulate any rethinking of the course of human evolution. Again, this can reasonably be ascribed to the gradualist mindset that prevailed when they were found: the new fossils simply needed to be slotted somehow—anyhow—into a preexisting framework, after which what they actually looked like could safely be ignored. Little wonder that more interesting things were emerging from archaeological field investigations than from the paleoanthropological laboratories.

Complex Lifeways

Before turning his attention to Arago, for example, Henry de Lumley undertook a salvage excavation of a site known as Terra Amata in the southern French town of Nice. This site, more securely dated than Arago to about 350 kyr ago, is interesting from several points of view. Among other things it contains, in the form of hearths, what may be the earliest evidence in Europe of the domestication of fire (although it’s possible that the Spanish sites of Torralba and Ambrona, probably as old or a little older, should take the laurels here; and recently the domestication of fire has been documented in Israel as far back as 790 kyr ago, at the site of Gesher Benot Ya’aqov). As importantly, though, Terra Amata apparently represented a seasonal hunting camp whose inhabitants built shelters of saplings placed into the ground in ovals and brought together at the top.

If this interpretation is correct, Terra Amata provides the earliest evidence from anywhere of such activity. Supporting evidence of the early construction of shelters was also reported during the 1970s from the German site of Bilzingsleben, at least 300 kyr old and probably more.



Artist's reconstruction of one of the hutlike structures at Terra Amata, France, with side cut away to show a hearth and interior debris. *Drawing by DS after a concept by Henry de Lumley.*

Throughout the postwar period the faunal succession in Europe was being refined and calibrated, and the earliest evidence for human occupation of Europe was being pushed back. Schoetensack's Mauer jaw was faunally dated to over half a million years ago, and until the mid-1990s it remained the earliest fossil evidence for ancient human presence in western Europe. Even at that stage, though, archaeological indications appeared to go back further. Aside from a dubious claim of crude 2-myr-old tools from a site in central France, several sites excavated during the last few decades of the twentieth century offer evidence for human activity in the western areas of Europe in the period following about 1 myr ago. Significant among these are the localities of Soleilhac and Le Vallonet in France, and Isernia La Pineta, in Italy, all of which contain simple flake tools and appear to be over 700 kyr old.

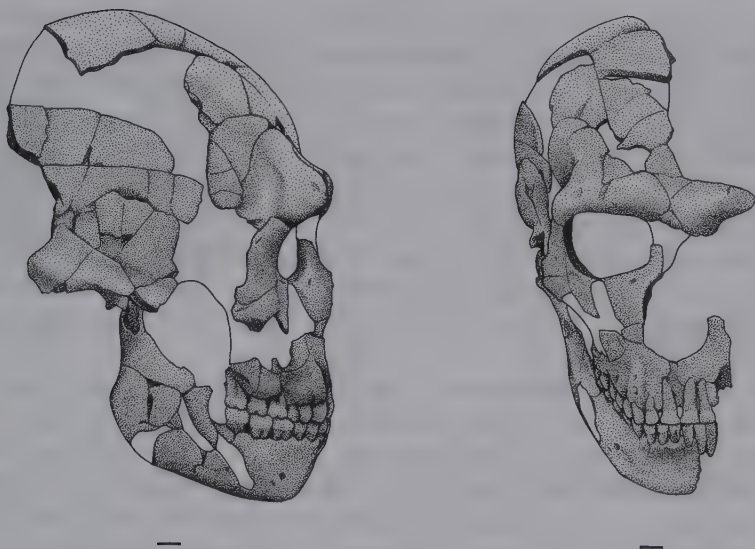
Further south, excavations during the early 1960s at the site of 'Ubeidiya, in Israel, produced Acheulean artifacts that were pretty firmly dated to about 1 myr ago or even earlier. This was considered good proof that by this time handaxe makers had managed to leave Africa, where these bifacially fashioned tools were first produced some 1.5 myr ago. It was thus maybe a little surprising that the earliest European archaeological sites were (and still are) bereft of handaxes, but it seems to be a general phenomenon that these tools get rarer the further away from Africa you go. Indeed, as far back as the 1940s Hallam Movius noticed that Paleolithic tool assemblages from India east to the Pacific rim tended to lack handaxes entirely, consisting instead purely of chopper and

flake tools. The significance of the "Movius line" between the handaxe-making cultures to the west and the non-handaxe makers to the east has long been argued over. One wrinkle is that it coincides more or less with the western distribution limit of bamboo—a versatile material that may well have served as an excellent substitute for stone. Well, maybe.

In Europe, handaxes were being produced occasionally by Arago times, and extraordinary abundances of these implements were reported by early workers at sites not much younger in France's Somme River valley, where Boucher de Perthes had made his original observations. Nowadays, though, it seems likely that this apparent great density of handaxes (which recalls a pattern widely seen in Africa) is in fact the result of selective collecting by nineteenth-century workers. More recent controlled excavations at European sites of Acheulean age have tended to show not only that a rather limited range of tools was being produced, but also that handaxes were not necessarily numerous among them—sometimes, indeed, they were rare or even lacking altogether. It's still unclear whether those sites not containing bifaces represent a separate cultural tradition from the biface sites, or whether they are simply a product of local circumstances or even sampling error.

No less obscure was the nature and timing of the "transition" between the Early Paleolithic period (in Africa, the Early Stone Age), to which the Acheulean belongs, and the Middle Paleolithic (Middle Stone Age) period that followed it. At some point over about 300 kyr ago, in both Africa and Europe, Acheulean cultures based on bashing a core into a particular shape began to be elbowed aside by stoneworking industries based on "prepared core" technology. This involved shaping a stone core in such a way that a flake of predetermined size and form could be struck from it at a single blow. With relatively little fuss this flake was then made into the finished tool. Such tools were generally scrapers of one kind or another, but quite often they assumed the form of handaxes. The prepared core technique had several advantages over earlier ways of stoneworking: one was a greater economy of material (for several flakes were often obtained from a single core), and another was the ability to control the shape of the flake; but probably the greatest advantage was that it produced a tool with a long continuous cutting edge.

Even today the dating of Middle Paleolithic sites tends generally to be rather poor, especially since they lie beyond the range of radiocarbon. For this reason alone it was hard to detect what was actually going on as handaxes began to decline and prepared core tools became increasingly common. There was no doubt, however, that this was not a smooth, gradual process. What's more, prior to the Neanderthals there was little direct evidence of the hominids who were involved in this technological changeover. It was only with the Neanderthals that the European human fossil record began to pick up in a significant way, and by the time they came along the Middle Paleolithic was firmly established; indeed, the Neanderthals' Mousterian culture was widely regarded as the apogee of Middle Paleolithic stoneworking.



Side and front views of the partial Neanderthal skull from St-Césaire, western France. Scales are 1 cm. *DM*.

Archaeological Transition

Until recently, the end of the Middle Paleolithic posed as many problems as its beginning. The Mousterian is followed in Europe by the Aurignacian culture, which is undoubtedly the product of early modern humans. However, at certain sites the early Aurignacian is overlapped by an industry known as the Châtelperronian: an industry having technical features in common not just with the Mousterian, but also with the Aurignacian and later "Upper Paleolithic" cultures. Notably, while flake tools were still important, about half the tools in the Châtelperronian kit were made on "blades": narrow flakes, more than twice as long as wide, which were retouched to produce a varied assortment of different tools. Blades were the hallmark of Upper Paleolithic stone technology in Europe (interestingly, they never caught on quite as much in Africa, although they were first produced there, perhaps as long ago as half a million years).

Who made the Châtelperronian? Neanderthals or moderns? Was the Châtelperronian the last phase of the Middle Paleolithic, or did it herald the Upper Paleolithic? As long as there was no firm archaeological association between this industry and human fossils, it was impossible to be sure. But in 1979 a find was made of a Neanderthal burial at a place called St-Césaire, in western France. The layer containing this fossil was late in time; even though its initial estimated date of 32 kyr was later revised backwards, to 36 kyr, this is still the most recent Neanderthal fossil that is both substantial and well dated. What's more, it fell squarely in the middle of a time gap previously

unfilled by western European human fossils of any kind. More important yet, the associated tool kit was Châtelperronian. For most Paleolithic archaeologists, the St-Césaire find solved the conundrum of the Châtelperronian: yes, it was the last gasp of the Neanderthals in Atlantic Europe (or was at least part of it). But why did this technology have such strong Upper Paleolithic features, in the very region where the late occurrence of Neanderthals demonstrated beyond doubt that they had not evolved into modern humans? One intriguing suggestion is that the western European Neanderthals learned by observation to make Upper Paleolithic-style blade tools, as early modern humans began to trickle into their territory at some time after about 40 kyr ago, bringing this new technology with them.

But even if this interpretation is correct, other evidence suggests as messy a picture for the departure of the Neanderthals as for the arrival of the Middle Paleolithic. At Portugal's Figueira Brava Cave, for example, fragmentary Neanderthal remains have recently been found in levels dated to about 31 kyr ago. These fossils, 5 kyr younger than those of St-Césaire, were found in an "evolved Mousterian" archaeological context and appear to provide good evidence for late but technologically pristine Neanderthal survival on the Iberian peninsula, as do those from the cave of Zafarraya in southern Spain, where Neanderthals survived to at least 30 kyr ago and possibly even until as recently as 27 kyr. Ironically, it is in Spain that we find some of the earliest evidence for the very early arrival of modern humans in Atlantic Europe: looking upon Iberia as the last redoubt of the Neanderthals against invading hordes of moderns arriving from the east begins to seem oversimplified. As usual, the plot thickens.

In the second half of the twentieth century the beginning of Neanderthal tenure in western Europe was also being pushed backward by new finds and new dates. In the late 1970s the back of a cranium was found at Biache-St-Vaast in northeastern France. The associated industry was described as Mousterian, and the site itself may be as much as 175 kyr old. The fossil shows "bunning" of the occiput and other features typical of the Neanderthals; despite its incomplete nature there seems to be no doubt that it represents a fully fledged Neanderthal individual. In addition, recent studies of the badly fragmented Ehrhingsdorf material initially described by Franz Weidenreich in the 1920s have indicated that some specimens at least possess a number of characteristically Neanderthal features. Further, dating carried out in 1982 using new techniques suggests that these fossils may be around 200 kyr old, though a more realistic assessment might indicate a broader possible time range, between about 110 and 200 kyr. By the early 1980s, then, it was possible to say that the Neanderthals were around in western Europe as a clearly recognizable group at least 175 kyr ago, and quite possibly well before that. Just how much before that was thrown into doubt in 1993 when Juan-Luis Arsuaga of the Universidad Complutense in Madrid and his collaborators reported the discovery of three quite complete hominid skulls from the site

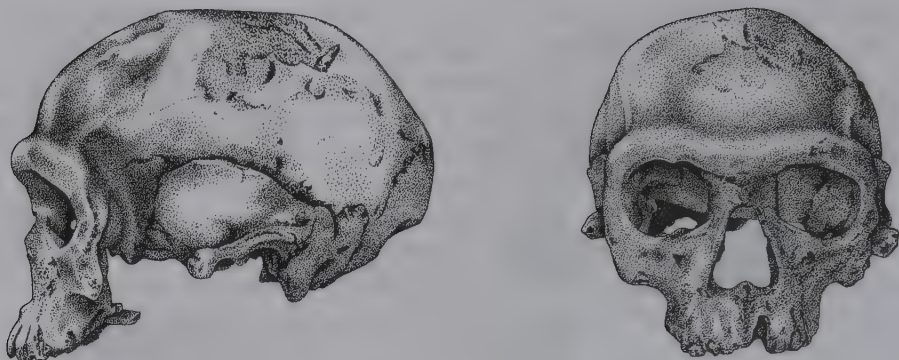


Side and front views of the cranium from the cave of Amud, Israel. Scales are 1 cm. *DM.*

of the Sima de los Huesos in the Atapuerca Hills of Spain, then thought to be some 300 kyr old. These specimens exhibit a number of Neanderthal features, and we will revisit them later.

East and South

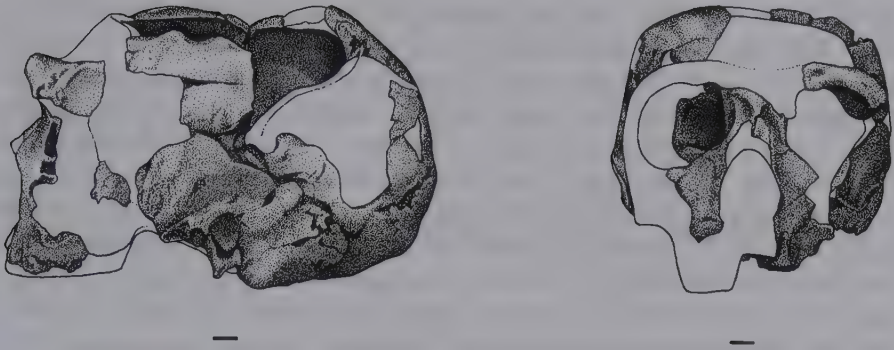
How about Neanderthals farther east? In 1961 excavations by a Japanese team at the Israeli cave of Amud revealed, in a Mousterian layer, a fairly complete skeleton of a young adult male Neanderthal with the extremely large cranial capacity of 1,740 ml (which may have to do with the fact that this is also the tallest Neanderthal yet discovered, with a stature of about 5'10"). Dating estimates hover around 60–50 kyr or a little earlier for this skeleton (and an infant skeleton very recently discovered). Both are clearly Neanderthal, and the adult is quite similar to the Shanidar specimens, confirming that even quite late Near Eastern Neanderthals failed to show the exaggerated characteristics of their kind exhibited by their "classic" contemporaries in western Europe. If the Amud individual was unusually tall, then another Neanderthal from the not-too-far distant and approximately contemporaneous Israeli cave site of Kebara was unusually massive: extremely strongly built, and with the largest lower jaw yet known for a Neanderthal. The Kebara fossil consists of most of the skeleton of a male individual who was apparently deliberately buried; sadly, it lacks the cranium even though the mandible is present. Very unusually, the hyoid (throat) bone is preserved, but that is a story we'll address later. The Kebara individual is the most recent Neanderthal we know of from the Near East, dating from about 50 kyr ago, and was found in a Mousterian archaeological context.



Side and front views of the Jebel Irhoud 1 cranium from Morocco. Scales are 1 cm. *DM*.

The 1960s saw important new finds elsewhere in the Mediterranean Basin, where over the course of that decade the Moroccan site of Jebel Irhoud produced two crania, a juvenile mandible, and a couple of postcranial fragments. At the time the date of these specimens was exceptionally uncertain (they are now thought to be more—maybe much more—than 130 kyr old), but their anatomy is extremely interesting. The more complete specimen has a lowish braincase and a rather big face with fairly noticeable brow ridges; and while the less complete one has a possibly more modern-looking front, the rear of the braincase has been viewed as rather primitive. First reported as Neanderthal remains, these specimens are nowadays viewed as vaguely “archaic” moderns, though they are clearly not modern *Homo sapiens*. Africa has still not produced any fossils that can plausibly be viewed as Neanderthal. The stone tools putatively associated with the Jebel Irhoud fossils are, however, of Mousterian type, as are those made by other early modern or modernish types in the circum-Mediterranean area, such as those from Skhūl and Jebel Qafzeh.

Around the time that the last discoveries were being made at Jebel Irhoud, more controlled excavations at the caves of the Klasies River Mouth were producing very suggestive evidence of early modern human occupation near the southern tip of Africa. The only human fossils found at the site are extremely fragmentary, but are nonetheless close to modern in form although some are more robust than others. Their archaeological context, however, is thoroughly Middle Stone Age. At Klasies, as in certain other southern African sites, there is an odd intrusion into the Middle Stone Age sequence known as the Howieson’s Poort industry. Middle Stone Age tools consist mostly of flakes struck from prepared cores, but the Howieson’s Poort culture produced lots of blades and tiny tools, thought to have been hafted, which are often referred to as “microliths.” This anticipates developments typical of the Late Stone Age in Africa (and that only cropped up in the latest phases of the Upper



Side and front views of the reconstructed partial cranium from Lake Ndutu, Tanzania. Scales are 1 cm. *DM.*

Paleolithic in Europe); but, occurring only over a short period about 70 kyr ago, the Howieson's Poort levels are overlain at Klasies by more nonmicrolithic Middle Stone Age deposits. Most of the human fossils from Klasies come from pre-Howieson's Poort sediments, and recent datings by various methods have suggested that the most ancient of them may be about 120 kyr old. Very intriguingly, Hilary Deacon of the University of Stellenbosch has suggested that these fragmentary Middle Stone Age humans from Klasies represent leftovers from cannibal feasts; he also finds evidence at the site for the kind of organization of the living space that is usually associated only with behaviorally modern humans.

Between 1940 and 1974 the site of Border Cave, between Swaziland and South Africa, produced several hominid specimens. All of them are without doubt anatomically modern; the problem lies with their dating, for the earliest discoveries were not made under conditions of controlled excavation. This unfortunately goes for the best specimen, an astonishingly modern-looking adult cranium that may be as much as 90 kyr old but might have been part of an intrusive burial from a later period. Its significance, then, remains moot, although it's not unlikely that it does provide supporting evidence for very early modern human occupation of southern Africa. Nonetheless, even if both the Klasies and Border Cave dates were reliable, the South African picture of Late Pleistocene human evolution was still not all that clear as the twentieth century drew to a close. For example, while a partial cranium found in 1932 at Florisbad, near Bloemfontein, is approximately equivalent in age to the Klasies fossils, it is distinctly archaic in form. In some respects it resembles the Ngaloba cranium found by Mary Leakey's team in the later deposits at Laetoli, dated at 130–150 kyr.

A couple of further African finds should be mentioned here. In 1973 Amini Mturi, of the Tanzanian Department of Antiquities, found a partial and badly fragmented human cranium on the shores of Lake Ndutu, at the western end of Olduvai Gorge. A best estimate would give this specimen an

age of about 200–400 kyr. As painstakingly reconstructed by Ron Clarke, the Ndutu fossil looks more modern, or at least more gracile, than the crania from Kabwe and Bodo, both of which may be of around the same age. There is a distinct if thinnish brow ridge, and the bones of the skull roof are rather thick, but the cranium is quite short from back to front, and may have been relatively high. Clarke himself has drawn attention to similarities to the rather younger German cranium from Steinheim, but the Ndutu form has none of the Neanderthal characteristics seen in the face of the latter. It's also possible that this fossil belonged to the same population represented by the approximately contemporaneous and rather small-brained (about 950 ml) specimen from Salé, in Morocco; interpretation of the latter, however, is hampered by a missing face and what seems to be an abnormally developed skull rear.

As this far from exhaustive list of individual specimens shows, there was throughout the 1960s and 1970s and beyond a steady background ticking of human fossil finds quite apart from the Leakey and Johanson discoveries that garnered most of the public attention. And every one of the fossils discussed in this chapter has its own particular importance for the reconstruction of the complex human past. But, to repeat, none of them in itself forced any major reevaluation of the accepted scheme of human evolution. At least in part, this was because paleoanthropologists were still pretty much stuck with the traditional way of doing things. Their role, as I suggested earlier, was still largely seen as a sort of service industry: stuffing new fossils into a convenient place in an established scheme.

Another reason, however, was quite simply that over these two decades new discoveries were coming in so thick and fast that paleoanthropologists didn't have the time or the perspective to digest them adequately. It's quite possible that the 1980s were an altogether more contemplative time in the science of human evolution because the pace of new discoveries slowed down somewhat. But although fewer new human fossils came to light, the impact of those that were found was nonetheless extraordinary. We'll look at those new finds in the next chapter.

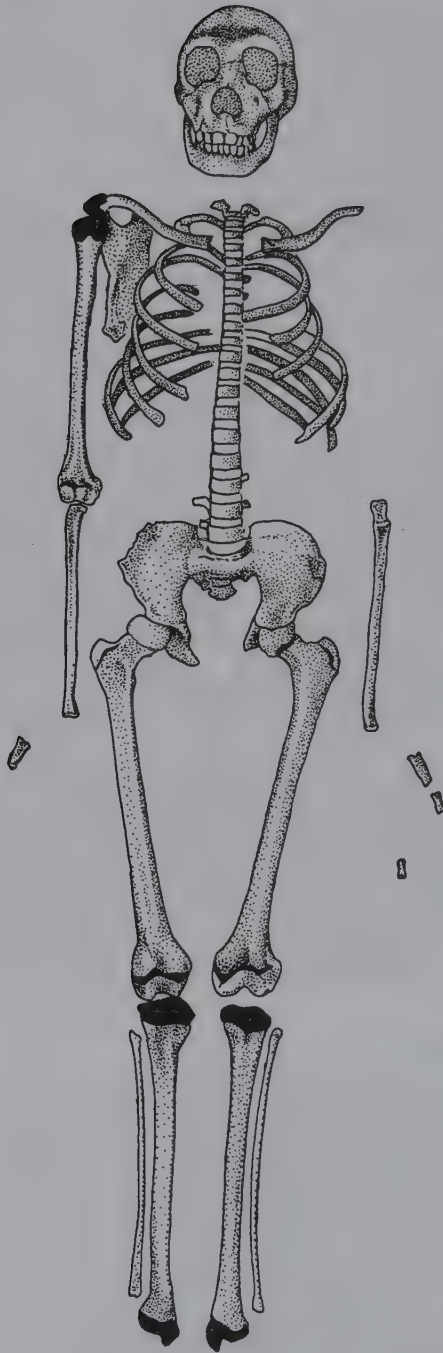
CHAPTER 14

Turkana and Olduvai—Again

By the time the 1980s came around, few still had any doubts that the human lineage had originated in Africa. And, quite possibly, fewer still doubted that *Homo erectus* stood square athwart the path from *Australopithecus* to *Homo sapiens*. Yet *Homo erectus*, despite the Koobi Fora group's recent discoveries, remained largely identified with Asia—until, that is, the forays by Richard Leakey's team into the hot, harsh badlands to the west of Lake Turkana began to pay off. In August 1984 a member of Leakey's team, the veteran fossil finder Kamoya Kimeu, found the first tiny fragment of a hominid skull at a site next to a dry stream bed extravagantly known as the Nariokotome River. Within a month or so, the group had recovered the greater part of the skeleton of a young male whose teeth had erupted about to the stage characteristic of a modern eleven- or twelve-year-old. This skeleton, dated to around 1.6 myr ago, and immediately assigned by its discoverers to *Homo erectus*, was yet more complete than that of Lucy, and incomparably more so than any other skeleton known from before the time of the Neanderthals. It was a unique find, and an astonishing one.

The “Turkana Boy”

What made it so amazing was that this young male totally contradicted the stereotype of *Homo erectus* as squat, heavy-boned, and powerfully muscled: a stereotype that, in the absence of substantial postcranial fossils, had endured ever since Dubois's time. Instead, the “Turkana Boy” (technically known as KNM-WT 15000) was both tall (about 5'4” at the time of his death, but it's estimated that had he lived to adulthood he would have achieved 6 feet) and slender. Indeed, according to Alan Walker who led the team that studied his skeleton, he was built overall very much like the people who live around Lake Turkana today—whose elongated limbs and slender bodies are designed to shed the heat load mercilessly imposed by the sun in those tropical latitudes. The prime importance to paleoanthropology of the Turkana Boy is that he represents the earliest kind of human we know of whose general body



The "Turkana Boy" skeleton (KNM-WT 15000) from Nariokotome, West Turkana, Kenya. *DS.*

proportions matched those of living people. Not that he was modern in all respects. One feature that initially attracted attention was the narrowness of the upper part of the canal through which the spinal cord runs. It was suggested that this showed limited nervous signaling to the thorax, indicating a lack of fine control of voluntary respiration and thus a limited ability to communicate using complex sounds; however, it is also possible that in this feature the Boy was pathological, and that this may even account for his early death. He was not barrel-chested, as we are, but had a somewhat upwardly tapering thorax (though less so than in Lucy, or an ape). His shoulder joints would thus have been closer to the midline of the body than ours are, and this is particularly interesting because it is helpful to be built like this when you are suspending yourself from tree branches, although it's not at all favorable in a striding biped that swings its arms for balance. The femoral heads are large, like ours, but the necks attaching them to the shafts are long, like an australopith's. This latter characteristic might be related to a rather narrow pelvic canal; the combination of the two factors might have enhanced stabilization of the hip, while, if the male can serve as an analogy for the female, it also restricted the maximum size of the newborn's head.

Which probably wasn't a problem. The skull of the Turkana Boy shows that his brain was not large; even at adult size, it would probably have been no larger than that of the slightly older ER 3733. His face, however, was more massively built and more projecting than the latter's; since 3733 is thought to be female, this difference was thought to be due to relatively strong sexual dimorphism in "early African *Homo erectus*." Interestingly, Holly Smith of the University of Michigan has shown that tooth development in the Boy had been rapid compared to modern humans, even if slowed down compared to apes and australopithecines. Thus it appears that the Turkana Boy may well have died after only about eight years of life, rather than after the 11–12 years that a modern human takes to achieve a comparable eruption of the teeth. The implications here are extensive, because the long developmental period of modern humans is strongly associated with many of the behavioral complexities that make our species unique in the world today. Below the neck, however, there's no denying that we have in the WT 15000 skeleton the first evidence of an essentially modern human anatomy. Nobody is going to dispute the Turkana Boy's abilities as an upright strider. So, once again, it seems that locomotor innovation had led the way among the evolutionary changes that ultimately led to the modern human condition. It certainly preceded any major technological improvements. For the Turkana Boy lived a full hundred thousand years before the inhabitants of the Turkana region began to make handaxes. His contemporaries made stone implements not very different from those that their predecessors had made almost a million years earlier.

Leakey and his collaborators were pretty categorical about ascribing their new skeleton and comparable Turkana fossils to the long familiar species *Homo erectus*. Allusions to the Zhoukoudian hominids, in particular, frequently

cropped up in their discussion of these materials. But even as they were making their great discovery, doubt was beginning to be cast on whether the allocation to *Homo erectus* was actually appropriate. At a 1984 meeting in Germany held to honor the memory of Ralph von Koenigswald (who had died in 1982), some of the participants questioned whether “early African” and “later Asian” *Homo erectus* were indeed the same thing. Peter Andrews, who summarized the proceedings, put the matter well. The problem in defining *Homo erectus*, he said, lay in the fact that it was “viewed at present as a grade of human evolution intermediate between the small brained early Pleistocene hominids and the large brained *Homo sapiens*.” In short, brain size was the key, and other characters were ignored. Yet brain size could not by itself be considered proof of membership of a particular species. Further, Andrews emphasized the point made by his London colleague Chris Stringer that many of the fossils lumped together into *Homo erectus* were linked simply by primitive characters inherited from a remote ancestry, rather than by derived ones that might indicate a special relationship. He pointed out that the Asian fossils were characterized by a suite of derived traits that were not present in the African forms and implied that the two populations actually belonged to distinct species. Examining the connotations of all this, Andrews found that the simplest scenario of *Homo sapiens* evolution “bypassed *erectus* in Asia,” thus echoing the conclusion that Niles Eldredge and I had reached back in 1975. Cladistics was beginning to bite.

Back to Olduvai

So were other new fossils. In 1985 Don Johanson and his collaborators received permission from the Tanzanian authorities to reopen fieldwork at Olduvai Gorge, from which Mary Leakey had retired several years earlier. In July 1986 they found the fragmentary remains of a hominid skeleton that they called OH 62. And fragmentary it was indeed. The skeleton had been eroding out of the Gorge deposits for a very long time—perhaps even for centuries, it was estimated—and was shattered into hundreds of tiny fragments, many of which were retrieved only by dint of laborious sieving of the sediments. But even with a total of some three hundred shattered bits, not much of the skeleton was preserved: the upper jaw (with some teeth) and some other skull fragments; most of the right arm and parts of both legs. Not exactly what the team had hoped for at the beginning of the excavation; but enough to draw some pretty startling conclusions about *Homo habilis*, the species to which it was assigned on the basis of resemblances in its teeth and palate. This assignment fit pretty well with its age and provenance: the site of discovery lay close to the bottom of the Gorge, not far from the famous Zinjanthropus site, and fell between two tuffs dated at 1.85 and 1.75 myr old. This made it almost exactly the same age as the original *Homo habilis* type specimens—and a bare couple of hundred thousand years older than the Turkana Boy.

The rather close correspondence in time between these two fossil individuals, both allocated to *Homo*, made the new Olduvai find seem especially remarkable. For if the Turkana Boy was tall and strikingly modern in his below-the-neck anatomy, OH 62 was quite the reverse. In life OH 62 had probably stood even shorter than Lucy; and it (we don't know what sex he or she was) had probably walked in a similar way, too, because its limb proportions seem if anything to have been even more archaic than Lucy's. In particular, OH 62 had had long, powerful arms, and Sigrid Hartwig-Scherer and Bob Martin of the University of Zürich soon showed that by a variety of measures its limb bones had closer resemblances to those of great apes than did Lucy's. All of this came as a surprise, to say the least, to a profession dominated by the gradualist mindset. Expectation had been that the body skeleton of *Homo habilis*, when found, would at least be intermediate in its morphology between those of *Australopithecus* and *Homo erectus*; this expectation was so powerful that, for example, some 2-myr-old isolated limb bones from east Turkana had been ascribed to *Homo habilis* purely on the basis of their rather modern appearance.

Of course, at least part of the problem lies with the unsatisfactory catchall nature of *Homo habilis*. In describing their new fossil, Johanson, Tim White, and colleagues noted that the original Olduvai Bed I *Homo habilis* had met with the objection that distinction from *Australopithecus africanus* was unwarranted. And they also claimed that new discoveries (including ER 1470 and 1813 and a new skull called Stw 53 that Alun Hughes had found in Member 5 of Sterkfontein in 1976—and which was thought to be a particularly good match for OH 62) had disposed of such objections. Yet in their very next sentence they noted that the new fossils had given rise to attempts to break up this larger sample into more than one species. For, despite the convenience it represented, rumblings were beginning to be heard by the mid-1980s that the newly enlarged *Homo habilis* might be a somewhat ill-assorted mish-mash of fossils belonging to more than one kind of early hominid. Thus at the "Ancestors" meeting held in 1984 at the American Museum of Natural History to inaugurate the first large public exhibition of original hominid fossils, the anatomist Bernard Wood had stated pretty flatly that there were at least three "nonaustralopithecine taxa" in the east African early Pleistocene. Similarly, in 1986 Chris Stringer published a paper called "The Credibility of *Homo habilis*" in which he found evidence for "at least three Plio-Pleistocene species of 'early *Homo*'" in east Africa (effectively, Turkana and Olduvai).

Stringer also noted that if you ignored cranial capacity, fossils such as ER 1470 and OH 24 looked more australopithecinelike than was generally acknowledged. Which brings us to the second part of the problem posed by *Homo habilis*—for, even if the gracile hominid fossils from Olduvai and Turkana are indeed excludable from *Australopithecus* (which is, I think, at least marginally justifiable), are they properly assignable to *Homo* (which in my view is much more debatable)? Here again we are heirs to an unfortunate legacy of the

Synthesis. We've seen that lumping of species is viewed by Ernst Mayr's many followers as antitypological, and therefore as by definition a Good Thing. As, to that extent, it is. But in paleoanthropology, no less than in other areas of human experience, no good idea avoids the fate of being taken to a ludicrous extreme. So lumping's converse, the creation of new species, almost inevitably came to be viewed by paleoanthropologists as a Bad Thing in principle. And this, of course, is why *Homo habilis* had had such a rough ride to begin with. We'll look again at this matter of species; for the moment let's just note that if new species are undesirable, new genera are unthinkable!

The Unthinkable Thought

But perhaps the unthinkable is just what needs to be contemplated. By the reckoning current in the waning years of the twentieth century, our family (or tribe, or whatever) contained only two or three genera: *Australopithecus* (plus *Paranthropus*, if recognized) and *Homo*. Interestingly, at the level of the body parts that fossilize, genera seem to be the *Gestalt* category of mammalian classification: Tattersall's Law only half-jokingly states that if you can tell two skulls apart at 50 paces, you have two genera, while if you have to scrutinize them close up to tell the difference, all you have is two species. Of course, this is an oversimplification, even a grotesque one; but it does express what seems to be a basic consistency: among mammals in general, the genus is the level at which the "family resemblance" among related species most clearly expresses itself (or is perceived by us). Genera, of course, are simply collections of species descended from the same exclusive ancestor (they are thus what is called "monophyletic"), but there's obviously a limit as to how inclusive a genus can be, or every living species would belong to the same one. And if a genus is thus no more than a monophyletic group of species, why be afraid of recognizing a sufficient number of them to express the morphological diversity that has accumulated within the group? There's absolutely no reason in principle at all to shrink from this exercise; but in paleoanthropology there was (and is) one very powerful practical one: we don't have an agreed-upon cladogram in which to discern the clusters of species that could usefully be separated off as genera without violating the criterion of monophyly. With any luck, one day we shall, but for the moment uncertainty and the inertia of tradition combine to make the multiplication of genera within Hominidae an almost taboo subject outside the confines of spectacular new finds. Too bad, but one should at least note that having to force *habilis* (and its relatives) into one or another of a mere two genera does little to enhance our understanding of the complexity of human evolution. It also makes it virtually impossible to arrive at a morphological definition of the genus *Homo* that has any substance whatever.

The most detailed analysis done of the *Homo habilis* situation as it existed by the early 1990s came from the pen of Bernard Wood. To him was entrusted the detailed description of all the east Turkana hominid crania,

teeth, and jaws; and Wood, a longstanding member of the Koobi Fora team, cleaved to approved procedures in the monograph that resulted. He clearly saw that there were more species among the hominid fossils than the party line suggested, but in this massive tome he refrained from giving them names. Subsequently, however, he was less inhibited. In evaluating the gracile fossils from Olduvai, he concluded that all could comfortably fit within the species *Homo habilis*, as defined by the fossils from low in Bed I. And if all of the Leakey Olduvai graciles belonged to *Homo habilis*, then so, almost inevitably, must OH 62—despite its extraordinarily archaic aspect. When he turned to Koobi Fora, however, Wood found a more complex picture. Some Koobi Fora hominid specimens, he concluded, were plausibly members of the same species: among these were the crania 1805 and 1813. Others, however, including the famous 1470 cranium, clearly had different affinities (within the genus *Homo*) and needed a new species designation. To the chagrin of some, such a designation already existed: *Homo rudolfensis*, based on a new species of *Pithecanthropus* created by the Russian anthropologist V. P. Alexeev to contain the 1470 cranium. Matching the cranial specimens with the few postcranial bones known from East Turkana is tricky, but a couple of femora, for example, are larger and more modern-looking than those of OH 62. These might plausibly be attributed to *Homo rudolfensis*, whereas a partial skeleton from Koobi Fora called ER 3735 is more archaic, with long arms reminiscent of OH 62. Thus the few postcranial bones known seemed to agree pretty well with the cranial and dental evidence that at about 1.9 myr ago two lightly built hominid species existed at Koobi Fora.

Although arrived at by a loyal and expert team member, this account of the Koobi Fora and Olduvai “early *Homo*” fossils differed greatly from Richard Leakey’s preferred interpretation. Although his own popular account of OH 62 stressed its incompleteness (while Johanson’s naturally enough emphasized the thought and diligence which was put into extracting the maximum of information from fragmentary material), Leakey nonetheless seized on this specimen as proof that about 2 myr ago at Olduvai there were two kinds of nonrobust early human: the big-brained *Homo habilis* represented by the type material, and a smaller, more archaic form represented by OH 62. At Koobi Fora, these same hominids were exemplified, respectively, by the large-brained ER 1470, with which were associated the more modern postcranial bones, and by the smaller-brained (ER 1813) and more primitively proportioned (ER 3735) form. In this way, Leakey was able to recognize three distinct kinds of hominid (including robust *Australopithecus*) that were ubiquitous in East Africa in the period that preceded his “early *erectus*.” And one of them was, of course, an ancient form of *Homo* that was shorn of the inconveniently primitive body proportions of OH 62.

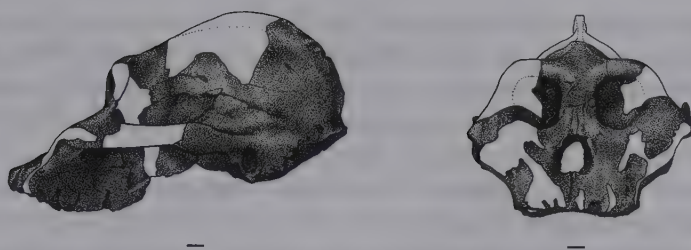
It is still early days to know what kind of pattern will ultimately be extracted from the mass of fossil material that has been attributed to *Homo habilis* at one time or another. And one can say the same for the African/Asian *Homo erectus*

question. For although Wood's study quite convincingly confirmed that the "early *Homo erectus*" material from Turkana is easily distinguishable from the Asian type material of *Homo erectus*, there is still an active lobby for retaining it in *Homo erectus*. But if it was different, it needed a name of its own; and the first name available for it under the rules of nomenclature was *Homo ergaster*, the name awarded by Colin Groves and Vratja Mazak in 1975 to the Koobi Fora lower jaw ER 992. An increasing number of paleoanthropologists is now happy with recognizing *Homo ergaster* in Africa as an entity separate from an endemic and ultimately terminal *Homo erectus* in Asia. But as we shall later see, this still understates the complexity of the actual situation.

The Black Skull

Meanwhile, west Turkana had yet another surprise in store. The excavation of the WT 15000 site was still going on when, in August 1985, Alan Walker picked up part of the skull of a robust australopithecine at a locality next to another dry stream bed, this one called the Lomekwi River. This fossil, however, wasn't just another robust australopithecine, for it was 2.5 myr old, a good half million years older than any other robust known from Kenya, and anything up to a million years earlier than *Australopithecus robustus* from South Africa. And, just as importantly, once Walker had pieced a more or less complete (though toothless) cranium together from numerous fragments, this specimen (affectionately known as the "Black Skull" from its dark patina, though it is more formally named WT 17000) was found to look very different from every other robust australopithecine skull known. One of the features for which all robust australopithecines then known were famous was the flatness of their faces, their shortness from front to back. Yet, as reconstructed, the Black Skull boasted a splendidly protruding, rather "dished" face, and a relatively sunken nasal region. Along with the elongated snout, for reasons of muscular advantage, came an equally long braincase, with a longitudinal crest concentrated toward the back. Plenty of anatomical detail, including chewing tooth roots of very generous proportions, indicated that this was indeed a relative of the younger "robust" australopithecine species, but the *Gestalt* of WT 17000 was hardly typical for the group.

Nonetheless, when Walker and Leakey announced this find in print, they tentatively placed it as a primitive member of the species *A. boisei*. In doing this they were clearly powerfully influenced by the prevailing paleoanthropological aversion to the naming of new species, and they were equally clearly aware of that fact, since they covered themselves by noting that future finds might necessitate putting WT 17000 in a separate species. A conference on the "robust" australopithecines organized in 1987 by Stony Brook University's Fred Grine provided a useful platform for discussion of this issue. At the conference the consensus emerged that WT 17000 did indeed require recognition as a species separate from *A. boisei*. But the consensus was also that a name



Side and front views of the “Black Skull” (KNM-WT 17000) from Lomekwi, West Turkana, Kenya. Scales are 1 cm. DM.

for this species already existed—a name that Walker and Leakey had, indeed, already mentioned in their initial paper. During the international expeditions to the Omo, back in the late 1960s, the French contingent had discovered a toothless lower jaw in sediments dating back to about 2.6 myr ago. This was much older than any other hominids then known, and, scrappy as the piece was, Camille Arambourg and Yves Coppens decided that it could not belong to any species (or genus—the French have always been less reticent in these matters than anglophones) that had already been described. So they called it *Paraustralopithecus aethiopicus*. Given the poor condition of the specimen, this new name was widely ignored at the time; but now that something of comparable age but more complete had been discovered, it excited new interest. The Ethiopian jaw was from a very much smaller individual than the Black Skull, and was in any case not directly comparable. But once a number of other Ethiopian specimens had been brought into the picture, as well as another lower jaw subsequently found at west Turkana, most of those attending the conference were prepared to accept a distinctive third species of robust australopithecine, exemplified by the Black Skull, which seemed to be represented by fossils ranging in age from about 2.8 to 2.2 myr old. By common consent, this form took the species name *aethiopicus*.

Graciles and Robusts

Another result of the Stony Brook conference was a broadening realization of just how different the “robust” australopithecines are from the “gracile” ones (quotation marks are used here because, as Grine is fond of pointing out, we don’t have enough evidence of the body skeletons of the “robust” forms to know how strongly built they were overall; all we know is that they had very large chewing teeth and supporting bony architecture). Despite this, although not everyone at the conference went along, a consensus was beginning to emerge that, way back in 1938, Robert Broom had been right to place his robust specimens from Kromdraai in a genus, *Paranthropus*, separate from *Australopithecus*. Accepting this distinction, there were now three species generally recognized within *Paranthropus*: *P. robustus* from South Africa

and *P. aethiopicus* and *P. boisei* from East Africa. However, this still left the relationships among the species of *Paranthropus*, and between this genus and *Australopithecus*, somewhat up in the air. Most paleoanthropologists by then accepted *A. afarensis* as the stem species from or close to which the later hominid species had emerged, but after that opinion diverged.

Given that a robust species was now known that was as old as *A. africanus*, it was hardly plausible (though still not impossible: the full time range of an extinct species can never be known with certainty) to place the latter at the root of the robust clade, as Johanson and White had done. And it was a little iffy to make *africanus* the progenitor of all later hominids, as had also been mooted. But sheerly on grounds of time it was still possible, for example, to argue that *A. afarensis* had given rise to the East African robusts on the one hand, and, via *A. africanus*, to the diverging South African robust and *Homo* lineages on the other; or to suggest that *afarensis* had simply thrown off two diverging *africanus/Homo* and *Paranthropus* lineages. The major question in early hominid phylogeny thus boiled down to whether the robust clade was monophyletic or not—whether or not the included species comprised all the known descendants of a single common ancestor. This is a problem that (despite the growing use of the name *Paranthropus*, which suggests monophyly) has still not been resolved to the satisfaction of all; it is, of course, bedeviled by the fact that we almost certainly have our basic units of analysis wrong. If there are two things we can be sure of, they are that, first, there are more early hominid species out there than we have yet, for whatever reason, been able to recognize; and, second, that among the species that we have accurately characterized, there's not one whose full time span on earth we know.

Faunal Turnover

One of the papers at the Stony Brook conference was delivered by the Yale (formerly Transvaal Museum) paleontologist Elisabeth Vrba, who had closely studied the evolution of mammalian (particularly antelope) faunas in Africa over the last several million years. She had noted that in various parts of Africa a remarkable shift in the fauna had taken place at around 2.5 myr ago: forest antelopes had become rare, to be replaced by species that graze on dry, open savannas. The conclusion was clear: some kind of climate shift had occurred that had turned much at least of the African forest to savanna. This turned out to fit neatly with geological findings indicating that a polar glaciation had occurred at just that time, decreasing average global temperatures by 10 degrees or more. Not only did temperatures fall, but the continents became more arid: this explained the nature of the vegetational change, which in turn accounted for the faunal shift. Vrba noted that it was about at this time, 2.5 myr ago, that *Paranthropus* appeared, that stone tools showed up in the geological record for the first time, and that the first fossil intimations of the genus *Homo* began to be seen (in the form of a skull fragment

found near Kenya's Lake Baringo by her Yale colleague Andrew Hill). Were these events related? Vrba thought so. And she also concluded that they were simply part of a larger pattern that had repeated itself over and over again during hominid history. For example, it was at about 5 myr ago that today's familiar antelope species began to proliferate on the African landscape, an event that also coincided with an episode of dramatic climatic cooling and drying, with a worldwide contraction of forests and expansion of savannas. And, of course, it quite possibly coincided with the emergence of the first hominoid bipeds out onto the savanna. For Vrba, then, climate shifts had dramatically affected the evolution of the human family, but as part of a much larger picture: she saw periodic changes of this kind as the cause of general "pulses" of speciations and extinctions in which our own ancestors, as well as those of a vast variety of other organisms, were inextricably caught up.

This is an attractive idea, which will live, die, or become transmuted as we come to know more about the timing of all these varied and putatively related events. It's also one that is firmly founded in evolutionary theory; for although it undermines traditional notions of gradual change, it fits well with what we know about how speciation occurs. The fragmentation of formerly continuous populations caused by the spread or contraction of savannas (or any other habitat) produces ideal conditions for speciation. And, along with innovation at the local level, it's speciation that is the engine of macroevolutionary change. Though the very notion is anathema to traditionalists, "retrogressively" invoking as it does a multiplicity of extinct hominid species, it is in fact highly probable that an increased speciation rate among hominids, due to the frequent climatic fluctuations of the Ice Ages (roughly, the last 2 myr or so), was at least partly responsible for the accelerated pace of change in the human lineage during the latter half of its existence.

CHAPTER 15

The Caveman Vanishes

The remarkable finds made in eastern Africa beginning in 1959 had tended to draw attention away from South Africa, where all the excitement in the “earliest ancestor” department initially started. Perhaps in part because of their humble origin as jumbled cave fill, as well as because of the difficulties of dating that this origin presented, the South African australopithecines had somehow seemed wanting in the romance that surrounds their brethren further north. Weeks and months spent in laborious rock bashing at a single locality like Sterkfontein tends to lack the glamour that accompanies striking out into a wild and remote landscape such as that of Hadar, where another reliably datable Lucy might lurk in every gully. Yet, without much fanfare, the inscrutable South African caves began in the 1960s to yield not only a remarkable crop of new fossils, but a story of their origins that was dramatically at odds with earlier interpretations.

Understanding the Caves

A leader in this renaissance of australopithecine studies in South Africa was Bob Brain of the Transvaal Museum. Brain was particularly interested in the way in which the cave sites had formed and in how the bones had accumulated as part of the breccia infill. In 1965 he reopened excavations at Swartkrans, the site from which robust australopithecines were best known, and by 1970 he was able to provide a new reconstruction of the way in which the cave had originated and subsequently filled with rubble. The original underground cavity, formed by solution of the dolomite rock by ground water, had become connected to the surface by a vertical shaft that may have descended beneath a rock overhang. Down this shaft, periodic rainstorms had washed all sorts of detritus, including dust, gravel, pebbles, and the bones of dead creatures. And, while Raymond Dart had concluded that the broken bones found at Makapansgat had resulted from the activities of bloodthirsty australopithecines, the Swartkrans bones looked to Brain much more like leftovers from



Artist's reconstruction of a leopard dragging away the young Swartkrans *Paranthropus* whose braincase was pierced by its canine teeth.
Drawing by DS after a concept by Douglas Goode.

the meals of carnivores. But if so, how had so many of them found their way into an underground cave, recently reexposed at the surface by erosion?

The dolomite limestones of the generally dry Transvaal continue to be weathered today, and situations like those at ancient Swartkrans are still quite common. The entrances to vertical fissures in the rock still form depressions into which water drains, with the result that in an otherwise rather treeless landscape it is not unusual to find trees growing in such places. Leopards often take their prey up into trees in regions where the carcasses are at risk from marauding hyenas; and it was leopards, Brain proposed in 1970, that were largely responsible for the bone accumulations at Swartkrans. The australopithecines, far from the hunters that Dart had envisioned, suddenly found themselves among the hunted. The fact that australopithecine postcranial bones were rare at Swartkrans by comparison with antelope bones or hominid skull fragments was attributed to the fact that primate postcranials are rather delicate: a leopard will typically consume an entire baboon, leaving only the skull, while much more will be left over from an antelope meal. In support of his idea, Brain was particularly pleased to find one partial juvenile *Paranthropus* braincase from Swartkrans that was penetrated by two identical and closely spaced holes: holes into which the canine teeth of a leopard jaw fit perfectly! When dragging its prey, a leopard will often grip the victim's head in its jaws; and the *Paranthropus* braincase eloquently recounted the story of a similar sad fate.

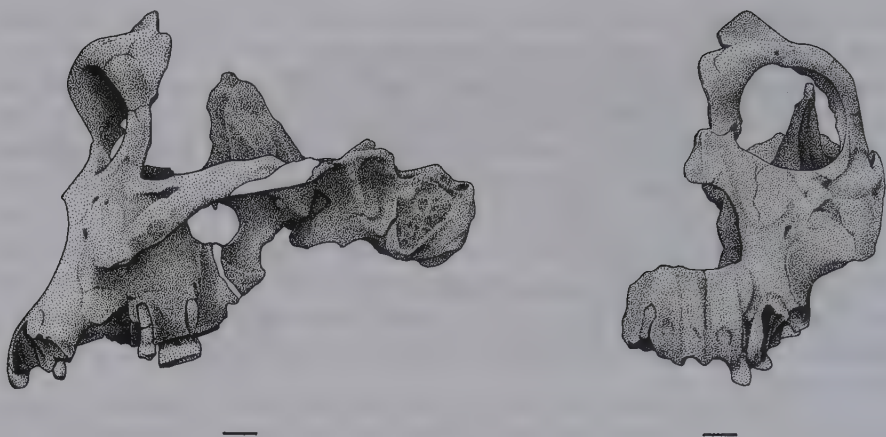
John Robinson, as we've seen, had noticed that a few of the hominid remains from Swartkrans were much more gracile than the robust ones for which the site was most famous; such fossils included the jaw for which he had initially coined the new name *Telanthropus*, but which he had later attributed to *Homo erectus*. Now, Brain confirmed that stone tools were also present at the site. These tools were described by Mary Leakey as most closely

resembling “developed Oldowan” implements from Bed II at Olduvai, though they tended to be bigger; among them were various kinds of choppers and a couple of bifaces. Unlike Olduvai, however, Swartkrans was emphatically not an activity site of the toolmakers: Brain gave cogent reasons for believing that the tools had simply been washed down into the cave along with other surface debris. Such debris had formed a conical deposit below the shaft leading from the surface down to the cavity; rocks and bones falling on to this cone were carried by their momentum to areas that might be quite distant from the opening. In this way, a very complex stratigraphy formed in the cave fill: one that took many more years to work out, especially since it became evident that the cave had in fact been subject to several episodes of deposition and erosion.

Diverse Records

In 1976 Brain was able to present an interpretation of the geology of Swartkrans by the Chicago geologist Karl Butzer that divided the breccia fill into two members (lithologically distinct units): Member 1 (with lots of hominids) and Member 2 (with many fewer hominids, but most if not all of the stone tools). Later excavations revealed a more complicated situation, however, and Brain ultimately divided Member 2 into four, with hominid fossils known only from the lower part of that sequence (Members 2 and 3). Dating of these various geological units (and of those at other South African cave sites) was also given a boost during the 1970s and 1980s by comparisons of their contained faunas with the newly available dated faunal sequences of eastern Africa: Basil Cooke was a pioneer in this, and studies of the antelopes by Elizabeth Vrba and of the monkeys by Eric Delson of the City University of New York and the American Museum of Natural History proved particularly useful. Such faunal comparisons suggested that the three Members at Swartkrans span the period from about 1.8 to 1.5 myr ago. Both *Paranthropus* and *Homo* fossils are known from Members 1 and 2, while only *Paranthropus* is known from Member 3 (though sparsely). It was notable, however, that while Swartkrans has produced the fossil remains of dozens of *Paranthropus* individuals, only six *Homo* fossils were known. Stone tools occur throughout, as do pieces of antelope bone (mostly long bones and horn cores) that have acquired a polish typical of bone artifacts that have been used for digging in the ground for roots, tubers, and so forth. The amount of wear on many of these is characteristic of prolonged use, suggesting that they were carried around for days at a time.

Who made or used these stone and bone artifacts? Either hominid might have done; but most paleoanthropologists feel that while it may well have been *Paranthropus* that used the bones for digging, it was *Homo* that made the stone tools. Not everyone, though—Randy Susman has studied hand bones from Swartkrans that were found during Brain’s excavations and has concluded not only that they indicate a capacity for precision gripping equal (if not



Side and front views of the reconstructed partial cranium SK 847, from member 2, Swartkrans, South Africa. Scales are 1 cm. DM.

superior) to that evinced by *Homo habilis* at Olduvai, but that they belonged to *Paranthropus*. If this is so *Paranthropus*, by far the most abundant hominid at Swartkrans, might plausibly be the stone toolmaker. Susman's interpretation has caused considerable controversy, however, and for the moment the authorship of the stone tools from Swartkrans remains debated. Interestingly, though, despite the fact that Member 3 has produced only australopithecines, it is from here that traces of fire are known. These occur in the form of burned stones and bones, heated to temperatures typical of campfires. Member 3 times were the only point in the early history of the cave at which hominid occupation of the cave entrance might have been possible, and this might account for the fact that burned objects only occur in that member. However, Brain prefers the idea that the introduction of fire took place between Member 2 and Member 3 times. As to the fire user (for Brain is as reluctant to conclude that a fire *maker* was involved as he is to affirm that the fire was used in cooking), few doubt that, despite the lack of fossils, it was the gracile hominid ascribed to *Homo*. Whatever the case, apart from some burned balls of clay, found in the late 1970s at a Kenyan locality called Chesowanja and dated to about 1.4 myr ago, there is no further association of hominids with fire of any kind until 790 kyr ago, when recent excavations at Gesher Benot Ya'aqov in Israel revealed a series of hearths in which domesticated fires had burned over an extended period of time. Certainly, the evidence for fire at Swartkrans and Chesowanja, whatever its implications, did not herald the control of fire as a regular feature of the hominid behavioral repertoire.

What species of *Homo* might have been the fire user of Swartkrans? Back in 1970 Ron Clarke realized that a Member 1 palate, ascribed to *Telanthropus*, actually joined with a facial fragment and a portion of temporal bone (both of which had been assigned to *Paranthropus*) to form part of the left side of the

cranium of a single individual of *Homo*, dubbed SK 847. Any species assignment remained in doubt, however, until Alan Walker visited South Africa in 1977, bearing a cast of the newly discovered KNM-ER 3733. The close resemblance of the two specimens struck both scientists, who agreed that they had before them an example of *Homo erectus*. This, of course, brought them into line with John Robinson, who had settled years earlier on a similar attribution for his *Telanthropus*. However, the question was opened again when doubts began to be voiced about whether the "early *erectus*" of Africa should actually be placed in that species; a reconstruction of SK 847 by Fred Grine, employing a mirror-imaging technique, highlighted some significant differences from *Homo ergaster* of East Africa. For the moment, then, the species identification of Swartkrans *Homo* must remain in doubt, but since it doesn't closely resemble anything allocated to *Homo habilis*, it will probably end up being placed in a new species seen as closely related to *Homo ergaster*.

In parallel with the work at Swartkrans, activity was also picking up at Sterkfontein. In 1966, during the celebrations for the centenary of Robert Broom's birth, Phillip Tobias and Alun Hughes presented detailed plans for reopening excavations at this classic *Australopithecus africanus* site. This work, which continues today under the supervision of Ron Clarke, had resulted in the collection of hundreds more hominid fossils (most, alas, fragmentary) by the time of Hughes' death in 1991. Most of these fossils are as yet undescribed, for Tobias dedicated the quarter-century following the discovery of Zinjanthropus to the massive labor of monographing the Olduvai fossils, leaving until later the equally monumental task of documenting the Sterkfontein collection. Notable exceptions, though, include the stw 53 cranium discovered in 1976 and initially attributed to *Homo habilis* and a few other fossils that were described by Ron Clarke during the 1980s. Initially thought to be younger, the 2.6-myr-old stw 53 is now allocated by Clarke and Kathleen Kuman to *A. africanus*, but Clarke also showed that a heavily reconstructed cranium (stw 253) from Member 4 possessed a number of features uncharacteristic of *A. africanus*. At about 2.5 myr old, this cranium comes from the same 2.5-myr-old deposits that had yielded the classical suite of *A. africanus* fossils. Reexamination of other Member 4 specimens convinced Clarke that there were, indeed, two kinds of hominid present there: a smaller-toothed form (classic *A. africanus*) with a rounded brow and a prominent nasal region, and a larger-toothed one (including stw 253) with a flatter brow and mid-face. Rejecting for solid reasons the notion that these two forms might merely be males and females of the same thing, Clarke concluded that two lineages were represented at Sterkfontein. Despite its rather expanded front teeth, Clarke discerned in the larger-molared form a precursor of *A. robustus*. As one sees more of this material it becomes plainer that Clarke is right in noting more than one species in Member 4 of Sterkfontein, but it seems likely that as more fossils are described and analyzed the picture will become more complex than even he has yet articulated.

Despite the relatively small number of hominid fossils known from Makapansgat a similar pattern seems to obtain there, too, with both smaller- and larger-molared individuals represented. Once again, reanalysis of the fossil bone assemblages suggests that they are the work of carnivores and scavengers, rather than of australopithecines wielding osteodontokeratic tools. With one single exception, all of the fossil hominid remains at Makapansgat come from the "Grey Breccia" deposits known as Member 3; the associated fauna suggests a date of around 3.0 myr, making Makapansgat the oldest of the classic South African australopithecine sites (except for a very early level at Sterkfontein, of which more later). The exact age of the original Taung skull remains a mystery, but the most recent faunal estimates suggest that an age of 2.8–2.7 myr is plausible, placing this site temporally in the middle of the classic *A. africanus* localities.

A Complex Picture

The South African australopithecine sites thus seemed to cover a span of as much as 1.5–2.0 myr (and now very considerably more: see the discussion in Chapter 18 of Clarke's latest discovery in Sterkfontein's Member 2). Specimens allocated to *A. africanus* come earliest in the sequence; *Paranthropus* appears next, at around the same time as *Homo*. During the long period covered by these sites, southern Africa appears to have been undergoing a general drying trend; in Makapansgat and Sterkfontein three times the vegetation of the highveld was probably rather bushy, with dense forest lining streambanks, while by Swartkrans times open savanna seems to have prevailed. Could this climatic shift explain the different dental adaptations of the robust and gracile types? Early on, John Robinson had suggested that the differences between the teeth of *Australopithecus* and *Paranthropus* were to be explained by diet: the gracile dentition was adapted for omnivory, while the robust one was that of a highly committed herbivore. In the 1980s Fred Grine, along with Rich Kay of Duke University, used electron microscopy to study the types of wear produced by chewing on the occlusal surfaces of the molars of the two types. Kay and Grine found that in *A. africanus* from Sterkfontein the tooth enamel was polished and lightly scratched, in contrast to the heavy pitting and gouging seen in *Paranthropus* from Swartkrans. Clearly, the two forms were eating different things, the latter specializing on harder, grittier substances: exactly the kind of vegetable edibles, such as roots and tubers, that are found out on the open savanna—and that digging implements are particularly helpful in obtaining. However, *A. africanus* also turned out to be a vegetarian, too, simply feeding on different kinds of plant products, perhaps mostly fleshy fruits.

Whether this correlation between climate, vegetation, and morphology is cause or effect remains to be clarified, especially by the application of new techniques that we will discuss later. But by the early 1990s Bob Brain was

able to suggest that the gap between Members 4 and 5 at Sterkfontein (very approximately the million years following 2.5 myr ago) represented a critical period of human evolution: one in which the hunted indeed became the hunters. His investigations suggested to him that, during the time when Member 4 was being laid down, the cave entrance was a lair of carnivores which dragged their australopithecine victims into its recesses. By Member 5 times, however, "the men had not only evicted their predators, but had taken up residence in the very chamber where their ancestors had been eaten." Yet, Brain added, "they were not more than amateurs in hunting...the nature of their antelope remains...suggests that they depended heavily on the kills of professional carnivores *before* they progressively developed their own prowess as hunters." The difficult nature of the South African cave sites made it hard at that stage of the game to go much further in assessing the capabilities of the earliest *Homo*. In East Africa, however, conditions for investigating this tricky issue were much more favorable—although consensus among archaeologists was nonetheless far to seek.

Experimental Archaeology

As work progressed at such East African sites as Olduvai and Koobi Fora, the range of questions that the archaeologists asked of the material at their disposal considerably broadened. Among other things, attention began to shift from the shape of the artifacts found to the technology that produced them. For the experimental production of stone tools by archaeologists taught them that the shape of a stone implement results at least as much from the form and nature of the piece of rock chosen to start with as from the actions of the toolmaker. So if you want to know about what was going on in the toolmaker's mind (and archaeological evidence for behavior tells you a great deal more about this than does the size and outside shape of his brain), the manufacturing process is much more informative than the end product. Mary Leakey, for example, put a great deal of effort into sorting Oldowan tools into a large number of different categories, identifying a whole "kit" of implements: spheroids, polyhedrons, discoids, choppers, and so forth. Most of these consisted of modified "cores" of one kind or another: cobbles from which flakes had been struck off. The assumption was that the cores—the pieces of stone that had actually been modified—were the implements that the toolmakers had intended to produce. Experiments, however, showed that quite likely it was the sharp flakes knocked off in this process that were the actual tools used for cutting. The idea that the different core types represented "mental templates" in the heads of the toolmakers did not seem to be borne out: they were simply byproducts of both use and of varying amounts of flake production using cores of different shapes, sizes, and materials.

But did this mean that that the Oldowan hominids, the makers of the earliest stone tools, were simply opportunists who struck flakes from whatever

pebbles happened to be handy where cutting tools were needed? The answer to this appears to be no. Mary Leakey had noticed early on that Oldowans had carried suitable rocks quite a distance to the places where she found the tools made from them. As it turned out, these early toolmakers were not highly selective; although they collected rocks that were suitable for tool making, they did not always make a great effort to amass the best possible materials. But at many localities in the Koobi Fora region, for example, the nearest natural sources for the lava cobbles turned into tools at archaeological sites turned out to be several kilometers away. Hominids must have carried these raw materials in over such considerable distances, and that flaking took place on site is shown by the fact that often flakes found close together can be joined up to reconstruct an intact core. Moreover, it is not uncommon for archaeologists to find more than one type of "foreign" rock at a given site, indicating that such objects had been brought in from several distant points on the landscape. Such activities on the part of early hominids require a degree of forethought quite out of the range of living apes, who, on those occasions when they make tools—most famously the stripped twigs used in "fishing" for termites—tend to pick up the raw materials at the spot where they are used.

Experiments carried out by Nick Toth of Indiana University suggest the same thing from another vantage point. Lumps of rock battered into roughly spherical shapes are quite commonly found worldwide at Stone Age sites, sometimes in large numbers. What these apparently deliberately shaped objects were made for remained a puzzle for many years, although they were often seen in earlier times as "bolas stones," tied together by thongs and thrown to entangle the legs of prey animals. By experiment, Toth was able to show that almost any lump of stone he chose would assume this spherical form after many hours of being banged against other pieces of rock. The distinctive shape was thus a passive result of use as a hammer and reflected no intent on the part of the toolmaker to produce a spheroid. Once more, then, the "mental template" idea failed. On the other hand, this finding did nothing to diminish the fact of the toolmaker's intent. For it took far more than a single session of tool making to produce a spheroid, implying that the toolmakers habitually carried their favored hammerstones around with them from place to place in anticipation of needing them.

One interesting experiment carried out by Toth, his Indiana University colleague Kathy Schick, and a group of psychologists at the Yerkes Primate Research Center concerned the ability of a living ape to make and use tools. Noting that it had become fashionable to look upon the early bipeds—roughly, anything prior to *Homo ergaster*—as "bipedal apes," Toth, Schick, and colleagues tried to determine how far a bonobo could be trained to flake simple stone tools. Their subject Kanzi, a star in communication experiments, showed an immediate interest in having sharp flakes available to cut cords that held a fruit-containing box closed. He got the idea of striking flakes from

a core, but even after many months of training he was still nowhere near the skill level of the Oldowan toolmakers. The latter clearly understood the major properties of the stones they worked, and selected the most effective points at which to strike an inevitably irregular core. Not so Kanzi, who never mastered the idea of striking stone at the optimum angle, though his technique has reportedly improved. His best products are rather like the "eoliths" that so confused early archaeologists: rocks randomly banged together and flaked as they rolled along riverbeds. Whatever long-term experiments with a range of apes will ultimately show, one still imagines that Samuel Johnson would find even the most sophisticated ape stone knapping less remarkable for how well it is done than for the fact that it is done at all. Toth and colleagues concluded from their initial study of Kanzi that the early hominid toolmakers had a much better cognitive understanding of what tool making is all about than any modern ape is able to acquire. And from that they hazarded that in hominid prehistory there must have been a stage of stone working that preceded the Oldowan, but that by its nature it would be difficult or impossible for archaeologists to identify or to discriminate from the results of natural forces. Still, these experiments give some idea of what one might need to look for.

Another aspect of experimental archaeology centers around how archaeological sites are formed and how they may later be disturbed and thus distort the story they contain. An archaeological site is just a place where there is evidence of early human activity, and the nature of the site depends on what activities were carried out there. In the Early Paleolithic the range of hominid activities preserved tended to be pretty limited, boiling down essentially to the making of crude stone tools, or to the butchering of animal carcasses, or both. Each of these processes can to some extent be mimicked by natural forces, particularly by water action that tends to concentrate objects that are simply lying around on the ground. Still, the creation of "artificial" archaeological sites by stone working and butchering at various points on the landscape can help in recognizing anthropogenic concentrations of stone and bone, whether pristine or altered by natural forces. But as much as this helps, there is still considerable disagreement over what most Oldowan sites tell us about how the earliest toolmakers were making a living.

Other Influences

Most Oldowan sites contain the bones of a variety of mammal species and body parts, some bearing cut marks made by stone tools or fractures that might well have been caused by hammering at them with a stone to get at the marrow. In earlier times this was taken as evidence of significant hunting prowess: the ability to kill animals of sometimes considerable size. But the paleoanthropologists Rick Potts and Pat Shipman noted in 1981 that, on bones from Mary Leakey's localities in the lower levels at Olduvai, cut

marks were often made over grooves already left on the bones by the teeth of carnivores, indicating that the carnivores had got to the carcasses first. What's more, Lewis Binford realized at around the same time that these sites also contained a preponderance of bones from body parts that bore little meat. From this and other evidence Binford concluded that the putative killer *Homo habilis* had in fact been a scavenger, attacking what was left of carcasses that carnivores had killed, feeding on their choice parts, and then abandoning them. On the other hand, analysis of the cut marks left on some of the bones suggested to the archaeologists Henry Bunn and Ellen Kroll that stone tools had in fact been used to dismember the higher-yielding parts of the animals. If this were indeed so, the hominids who did the job either must have freshly killed the animals they dismembered, or were effective enough to chase away the carnivores who had. Bunn's and Kroll's reading of the evidence has, however, been disputed on a number of grounds; if pressed, most archaeologists would probably plump at present for a relatively humble scavenging role for the first stone toolmakers. Or they would at least remain agnostic on the matter. To place all this in perspective, however, it is wise to bear in mind that, even in recent times, meat has tended to make up only a minor proportion of the diet of hunting and gathering humans except in highly specialized situations.

What about the localities themselves? The concentration of bones and artifacts at some well-preserved early Stone Age sites certainly suggests that ancient hominids returned to them repeatedly, although their reasons for doing this are still obscure. As we've seen, Glynn Isaac's early notion that they represent places where food was brought to be shared out has been more or less abandoned. But, as Kathy Schick has pointed out, it still appears that these locations were "favored" by early hominids. Perhaps such sites were simply centrally located within group territories, or maybe they offered shade or sleeping trees or a good view of the surrounding landscape and potential predators. Or maybe they did serve some more specifically social function. Some sites, it's been suggested, may have served as depots for stones suitable for flaking; this would have minimized the carrying of such items that would have been necessary. And at the simplest end of the spectrum, other sites may simply have been places where animals were butchered where they lay. What seems sure is that there is no good evidence anywhere for very early structures of any kind. The stone circle at Olduvai site DK may well have been caused by fracturing of the underlying lava by the roots of a tree, and is in any case rather indefinite; although similar phenomena have been reported from elsewhere, there really are no convincing candidates for hominid-built structures until very much later in the archaeological record. As we've seen, the same goes for fire. The evidence for burning at Swartkrans in South Africa, and at Chesowanja and one other locality in Kenya at around 1.4–1.5 myr ago, does not add up to firm evidence for the deliberate manipulation of fire, and certainly did not inaugurate an "Age of Fire."

I've already noted that at about 1.5 myr ago, some time after the appearance of *Homo ergaster*, handaxes and cleavers appear in the archaeological record, ushering in the Acheulean industry. Finally, here is a tool type that was unquestionably made according to a "mental template" that existed in the minds of the makers. For few dispute that handaxes were no chance result of flake production, and at some sites these bifacially flaked and carefully shaped tools have been found in extraordinary abundance, with a remarkable consistency of size and shape. Although rather unwieldy when large, and sometimes very heavy, handaxes represented an astonishingly successful technology, spreading throughout all inhabited areas of the Old World apart from eastern Asia and remaining in production for well over a million years. Exactly what kind of cognitive advance the making of such tools represented is not clear. Indeed, it is not at all obvious that cognitive advances (that is to say, differences in conceptualizing abilities) go hand in hand with technological advances; after all, the latter have ultimately to result from an innovation by an individual, who is unlikely to differ wildly in cognitive capacity from his—or her—parents. Any technological advance, in other words, has to be within the cognitive abilities of individuals belonging to the species concerned; it can't enlarge those abilities.

Experimental work by Peter Jones and by Toth and his colleagues suggests that the handaxe form was best adapted to the task of butchering large animals (though it has been shown that simple Oldowan flakes are capable of cutting through the inch-thick skin of an elephant, and microwear analysis of such tools has shown that they were used for cutting meat and soft plants, as well as for working wood). Picks (slender-tipped handaxes) seem to be particularly good for digging. Nonetheless, despite the utility of handaxes in butchery, there is still some question about the lifestyle of the handaxe makers. Traditionally, such handaxe sites as Spain's Torralba and Ambrona were viewed as places where very large mammals were killed; but more recently authors have emphasized the role of carnivores and other natural forces in creating the assemblages. Similarly, eastern African handaxe sites with the remains of large mammals can often be explained by factors other than hominid predation. The upshot of new excavations and new analyses of older evidence in the last quarter of the twentieth century was an outbreak of archaeological fence-sitting on the matter of the hunting prowess of Acheulean hominids. Particularly interesting in this connection was Binford's analysis of the bone assemblages from Zhoukoudian, which, as you'll recall, Franz Weidenreich had interpreted as the result of hominid carnivory and cannibalism. According to Binford, the activity of hyenas was particularly important in creating the bone accumulations at the site, and may even have been responsible, along with geological factors, for the broken-up condition of the human remains. In this connection it's worth noting that the dark "ashy" sediments at Zhoukoudian that were thought to have been evidence of fire were also recently shown to have been naturally occurring deposits of manganese.

The Neanderthal View of the World

Binford's interests also extended to later periods of human evolution. While studying the "Mousterian problem" he became convinced that modern hunters and gatherers were an inappropriate model for trying to understand Neanderthal lifestyles, which, he believes, were in fact entirely different from anything evinced by modern humans. Analyzing bones and tools from levels dating from approximately 125–70 kyr ago at the site of Combe Grenal, in western France, Binford rather controversially found that at each level two separate concentrations of artifacts and bones occurred. In "nest" areas were found plenty of ashy materials, which indicated that fires had burned there (though there were no hearths), plus plenty of simple flake tools made from local stone and marrow bone fragments. Elsewhere were scattered smaller concentrations of bone, with more sophisticated stone tools, such as retouched scrapers, that were made from materials brought in from distant localities. What's more, the animal bones associated with the scrapers were regularly those of species that lived in environments where the stone came from; the conclusion was that the food remains also had to have been carried in from some considerable distance away. Binford hazarded that the nests were where females lived, and that the scraper sites were made by males; to cut a long story short, if true, this suggested that males and females led largely separate lives, the males ranging widely and returning only occasionally to join the females, who led more sedentary existences. For Binford, there was no evidence at Combe Grenal that Neanderthals lived in families defined as reproductive units in which resources were shared among all members. Binford's interpretation of Combe Grenal was more widely criticized than hailed. But there can be no doubt that he was on the right track when he questioned whether Neanderthals could usefully be understood in terms of our own propensities for social organization.

Binford also inferred differences from modern people in the distribution on the landscape of Neanderthal sites. These did not occur in areas of extensive grasslands where vast migrating herds moved great distances in predictable patterns and where they were widely exploited by early modern people. Instead, Neanderthal sites were concentrated in areas of varied vegetation where the resources, if more limited, were also more constant and required less foresight in their exploitation. Systematic hunting of large-bodied mammals, Binford believed, is a monopoly of behaviorally modern *Homo sapiens*. This is a provocative hypothesis, and one that is generally consistent with what we can otherwise tell from traditional sources of data. It is not, however, necessarily substantiated by new, high-tech methods of analysis that we will look at shortly.

The archaeological record shows clearly that the Neanderthals perceived the world differently from the way we do and were generally less innovative than the modern humans who replaced them. But there's no denying

that, like us, they had large brains. Does this imply that, even if they were rather unimaginative, they possessed other human features such as language? It turned out that neither the size nor the external appearance of the brain was of much use in answering this question: there was and is simply no way of reading function with adequate precision from the bumps and fissures on the outside of the brain (and still less from brain casts). So no help was forthcoming from that direction. Speech, however, is a (somewhat) different matter from language as such. For to produce the sounds that are associated with modern articulate speech, you need specialized peripheral equipment as well as a language-ready brain. Notably, you have to have a larynx (voicebox) that is situated low in the throat and that is thus connected to the oral cavity above by a long section of tubing (the pharynx). This long pharynx can be manipulated by the muscles of the throat to modulate the vibrations produced at the larynx, and thereby helps to make the basic sounds on which articulate language depends. Primitively, the base of the hominoid (indeed, mammal) skull is flat. This flatness reflects the presence of a high larynx and a short pharynx, limiting the range of sounds that can be made. Among modern humans, in contrast, space for a high, looping pharynx is created by bending the base of the skull downward, creating a characteristic flexion.

In the early 1970s, the anatomist Ed Crelin and the linguist Philip Lieberman had the idea of reconstructing the vocal tracts of fossil hominids using the shape of the skull base as a guide. Using Marcellin Boule's original reconstitution of the La Chapelle Neanderthal skull as a first example, Crelin made a model of the airways; Lieberman then used this model in a computer simulation of the sounds the airways could produce. The model proved deficient in three of the most basic sounds associated with articulate speech. This work was subsequently extended and refined over the 1980s, notably by Crelin's former student Jeffrey Laitman, now of New York's Mount Sinai School of Medicine, who has noted a trend among the hominids. Among the australopithecines, Laitman found, the skull base is flat, just as it is in apes and all other mammals. But in *Homo ergaster* there was a slight but measurable flexion; and the 150 kyr-plus Kabwe skull (if not that from Petralona) looked to him almost modern in this respect. The Neanderthals, however, bucked the trend. A recent reconstruction of the La Chapelle skull does show more flexion than the original Boule version; but it's definitely much less than what we see in Kabwe. A similar story is told by the La Ferrassie skull, also about 50 kyr old, although certain earlier Neanderthals, such as that from Saccopastore in Italy (ca. 100 kyr), appear to have somewhat more flexed skulls.

Lowering of the larynx to permit refined sound modulation is not an unalloyed blessing: the high-larynx configuration permits simultaneous breathing and swallowing, and this eliminates the possibility of choking to death, an inconvenience to which modern humans are regrettably subject. Changes of the airways in the modern direction thus involve a distinct tradeoff, so in terms of evolutionary advantage we're clearly in a gray area here. One

possibility was that the apparently primitive high larynxes of the putatively cold-adapted Neanderthals were in fact specializations—one way of dealing with consistently cold, dry inspired air. Well, maybe. Hope, it must be said, lingered until the beginning of the 1990s that the discovery of fossil human hyoid (throat) bones would help with the problem of early speech by providing more direct evidence of throat structure. However, a beautifully preserved Neanderthal hyoid belonging to the Kebara skeleton succeeded only in declenching an appropriately vociferous argument over its significance. What there is of this bone looked pretty modern, but the problem was that only a small part of the whole hyoid actually ossifies; what this element's long-vanished cartilaginous portion looked like was anyone's guess. But we shall shortly see that, however the hyoid argument works out, when you put the cranial evidence together with what the archaeological record suggests about the capacities of the Neanderthals and their precursors, it's hard to avoid the conclusion that articulate language, as we recognize it today, is the sole province of fully modern humans.

CHAPTER 16

Candelabras and Continuity

For most of the second half of the twentieth century, the paleoanthropological limelight was almost completely monopolized by the search for our earliest hominid ancestors. The origin of our own species, *Homo sapiens*, though of equal or even greater intrinsic interest, just didn't seem to have the same inspirational power. Perhaps this was in great part because paleoanthropologists of the period weren't able to agree on what *Homo sapiens* is (or was), although most of them were prepared to include in this species a motley assortment of fossils going well back into the Middle Pleistocene, a half million years ago or more. And in part, I suppose, it was due to the fact that the adherents of the Synthesis simply didn't expect to find the origin of *Homo sapiens* in an event as such. Rather, they expected a slow transformation, in the long course of which it would be impossible to identify any single point at which full humanity emerged. In retrospect, it seems almost inevitable that it was to the elaboration of this notion that the proponents of the single-species hypothesis retreated, once it became no longer possible to deny that in earlier times two and probably more hominid species had coexisted in Africa. And in doing this, they performed the valuable service of drawing attention back to the question of modern human origins.

The Multiregional Model

You'll recall that before the Second World War, Franz Weidenreich had developed the theory that the various major modern groups of mankind (he explicitly recognized four: Australian, Mongolian, African, and Eurasian) had distinct origins going back to the time of Pithecanthropus and beyond. Each of these lineages had evolved independently, at its own pace. But if so, how had they all managed to remain members of the same species? Weidenreich had the answer. "The tendency to transmute the primitive types into those of recent man," he wrote in 1939, "must be considered inherent to the form as such." In other words, Weidenreich invoked a form of orthogenesis—an innate urge to evolve toward a particular goal—as a mechanism to explain how several

distinct human lineages had managed to change independently, yet arrive at more or less the same point. Even in prewar China this explanation must have sounded more than somewhat old-fashioned; but Weidenreich was simply seeking a justification for something that he believed he saw in the fossils. In terms of those fossils themselves, Weidenreich's "Australian group" was the offspring of a lineage, ultimately descended from *Gigantopithecus*, which passed from *Meganthropus*, through *Pithecanthropus*, and reached early modernity with Dubois's Wadjak cranium. *Gigantopithecus* also gave rise to a lineage that passed from *Sinanthropus*, through a series of unknown intermediates, to the Upper Cave skulls from Zhoukoudian, and ultimately to modern Chinese and other eastern Asians. Modern southern Africans stemmed from a series of predecessors that included the Broken Hill cranium and, later on, Broom's Boskop skull. Finally, in Europe and western Asia the sequence ran from unknown precursors through the Tabūn Neanderthals, the Skhūl early moderns, and the Cro-Magnon remains before culminating in modern Eurasians.

For some reason, Weidenreich chose to represent all this in a densely gridded and regularly geometric diagram that seemed to suggest that many more parallel lineages had in fact existed alongside the basic four that he named and that showed diagonal connections at regular intervals between them all, presumably intended to represent interchange of some kind. This diagram is at once elegant geometrically and of a mind-boggling complexity biologically; and like any formulation in which every possible combination of points is joined by some combination of lines, it is susceptible to fundamentalist interpretation in a vast variety of different ways. At a conference I attended in Jerusalem around 1990, I was astonished to find myself attending a session devoted to the vigorous exegesis not, as I'd expected, of whether Weidenreich had been right or wrong, but of how badly Harvard's Bill Howells had misconstrued Weidenreich in his textbook *Mankind in the Making*. In this volume Howells had dubbed Weidenreich's view the "candelabra" model of human evolution, based on a simplified version of Weidenreich's diagram that looked something like a candlestick bearing four candles. He contrasted this to the alternative "hat rack" theory, where a single central stem sprouted off a few side branches. In the candelabra the candles, or parallel lineages, ran just as Weidenreich had indicated; Howells' sin was to have made the diagram readable by eliminating the diagonals of Weidenreich's original. Many of those present at the conference were greatly upset by this for, even though Weidenreich himself had not been excessively concerned with genes, his later disciples were. And, as we'll see in a moment, the diagonals in Weidenreich's diagram had now become the key to their new interpretation of the master's pronouncements. Perhaps Jerusalem was an appropriate locale for this scientific farrago; the tone of the discussion was positively Talmudic and brought home to me very clearly how ingrained received scientific wisdom can become, as well as how important it is to find a respectable pedigree for one's ideas.

Howells, who died in 2005 at the age of 97, was at the time of the Jerusalem conference a much revered elder statesman of paleoanthropology; and the vehemence of the attacks on his candelabra diagram (more than 30 years after the fact) may, I think, have been motivated much less by its substance and authorship than by the fact that the candelabra coincided with the version of Weidenreich's views propounded (and inadvertently discredited) by the University of Pennsylvania anthropologist and noted TV personality Carleton Coon. In their original form, it must be said, Weidenreich's notions had attracted rather little attention; as Coon himself said in the introduction to his *The Origin of Races*, published in 1962: "Like other premature comets of science, Weidenreich's idea flashed across the sky and was gone, obscured by the clouds of incredulity released by his fellow scientists." These incredulous fellow scientists, Coon continued, believed that "the living races of man could have become differentiated only after the stage of *Homo sapiens* had been reached." Coon thought otherwise, and exhaustively scrutinized virtually every human fossil then known in an attempt to show that five distinct human "racial lines" (add the San of southern Africa to Weidenreich's four) could be traced back as far as the origins of the genus *Homo* itself—as Coon understood it over 30 years ago, back to *Homo erectus*. But although he demonstrated to his own satisfaction (and, by his account anyway, to that of two of the giants of the Synthesis, Ernst Mayr and George Simpson) that human subspecies could be older than the human species, few other paleoanthropologists agreed. Indeed, Coon was widely reviled for propagating a racist doctrine. The strength of this reaction was understandable, due as it was in great part to an emotional rejection, in the decades following the horrors of the Holocaust, of the notion that *Homo sapiens* was anything but the most closely knit of species. Less viscerally, though, it also reflected the entirely accurate perception that different lineages could hardly evolve separately into the same new species.

The objectors were actually right on both counts; but, as it ironically transpired after the furor over Coon's book had died down, it was precisely the inheritors of the good-hearted liberal tradition, the guardians of the Synthesis that had seen such anachronisms as orthogenesis off the stage, who were to resuscitate Weidenreich's ideas. They managed to distance themselves from the odium of Coon and the candelabra by returning to the pristine purity of the founding document, in which they reinstated the diagonals of Weidenreich's original diagram. These now represented gene flow between adjacent populations, even as local lineages followed their own independent evolutionary paths. Genes were, it was said, exchanged between neighboring lineages in sufficient quantities to ensure that all remained part of the same big happy species.

Thus was born the "Multiregional Continuity" industry that has employed so many paleoanthropologists in the years since the demise of the single-species hypothesis, and that stands as an enduring testament to the bewitching power of the neodarwinism of the Synthesis. The most cogent early statement

of the idea of multiregional continuity was put forward in an article published in 1981 by Alan Thorne of the Australian National University and Milford Wolpoff of single species fame. In this work Thorne and Wolpoff argued that a distinctive regional population could be traced in Australasia for almost a million years, from the time of the Javan Sangiran 17 specimen to early Australian *Homo sapiens* from the Kow Swamp site (ca. 10–14 kyr). In later publications these authors and their students and collaborators, the latter including the distinguished Chinese paleoanthropologist Wu Xinzhi, have broadened the original idea of continuity in island Asia and Australia to embrace other regions, most notably China, but also virtually everywhere else in the Old World. The basic idea underlying all this is that when hominids first emigrated from Africa at around a million years ago, they spread throughout Eurasia. As these émigrés (*Homo erectus* by Thorne and Wolpoff's reckoning at the time) encountered unfamiliar environments in their new homes, they rapidly evolved area-specific adaptations to help them cope more successfully with their unaccustomed new habitats. In this way, regional physical distinctions became rapidly established; these then lingered and were extended over a vast period of time, even as gene exchange between adjacent populations helped keep all hominids united in a single species. Even the rather daunting prospect of explaining how different stocks could evolve separately into the same new species turned out to be no problem for Thorne and Wolpoff: when they finally realized the true difficulty that independent crossings of the same species boundary represented, they found a solution in the simple expedient of following Mayr's advice and making *Homo erectus* simply a primitive form of *Homo sapiens*.

If the tone of this account seems slightly less dispassionate than most of what has preceded it, please forgive me. I hope I have managed not to mangle the Multiregional Continuity idea any more than extreme compression necessarily requires, and I hope even more that I have not given the impression that its exponents were and are anything other than highly capable and knowledgeable scientists. But this viewpoint does seem to me to illustrate, better than any other current example, the extreme parochiality with which paleoanthropology is cursed. Up to this point, it appears, we paleoanthropologists have proven unable as a group to shed our major historical burden: the birth of our science out of the study of human anatomy, rather than out of the comparative anatomy and geology from which other areas of vertebrate paleontology emerged. Under the heavy hand of this heritage, which places our species at the center of the academic universe, we seem incapable of seeing *Homo sapiens* as simply one more species among many. We constantly seek special explanations for ourselves. And, perhaps worst of all, we are afflicted with a tradition of looking for variability in our collections of fossils, rather than for diversity. This may sound like a minor quibble, but our "search image" is actually crucial to the way in which we interpret the fossil evidence of our past. Variability (within species) and diversity (among

them) are not simply two sides of the same coin. As human anatomists, we are acutely aware of the fact that *Homo sapiens* is highly variable, both within and among populations, in virtually every physical trait. And we enthusiastically overextend this yardstick into the business of classifying our fossils. Add the conventional gradualist view of human evolution to an exquisite sensitivity to anatomical variation, and it's not surprising that Thorne and Wolpoff didn't have a problem in squeezing *Homo erectus* and *Homo sapiens* into the same species; after all, the revered Ernst Mayr hadn't, and to the transformationist mindset the boundary between ancestral and descendant species is anyway purely arbitrary.

The Diversity Perspective

Paleontologists in other subdisciplines have a different perspective, however. For in the nature of things they are concerned with lots of species. Nobody, except perhaps an exterminator, can make a career studying one species—or one genus, or one family—of rodent. Paleontologists studying nonhominids must quite obviously be concerned with diversity: the extraordinary variety of species which evolution routinely throws up within every successful major group. Diversity is an inescapable fact of nature—unless you happen to be obsessed with one species alone. Yet just because there is only one hominid species in the world today, are we justified in concluding that there has only ever been one? The fossil record at Koobi Fora tells us otherwise, and I shall argue later that it is only with the arrival of ourselves—behaviorally modern *Homo sapiens*—that an entity of a truly unusual kind appeared on Earth. For now, it's sufficient to note that there's no good reason to look at our fossil precursors with eyes any different from those we focus on any other mammal species. And it was in the spirit of that realization that, in the mid-1980s, I began to look again at the human fossil record.

One thing that was bothering me at the time was the problem of recognizing species in that record. Species are the basic unit of evolutionary analysis, making the grouping of fossils into species the most fundamental process in paleontology. If we get our species units wrong, our further analyses will be invalidated all the way down the line. But there is a basic quandary here, because speciation—the establishment of definitive genetic isolation between related populations—is an event that does not necessarily have anything to do with morphological change, certainly at the level at which we are able to detect it in the fossil record. Little as we know about the actual mechanisms of speciation, it's clear that they involve events which have to do with reproductive compatibility at some level or another, and not with adaptation as such. In other words, whatever its underlying mechanisms, speciation is not simply a passive result of morphological change under the guiding hand of natural selection. This being so, a species may on the one hand accumulate a large amount of adaptive or random morphological variation while still retaining its

reproductive cohesiveness. On the other, however, that cohesiveness can quite easily be disrupted in the absence of appreciable morphological diversification. Pity the poor paleontologist; for if speciation has nothing necessarily to do with bony or dental morphology, which is essentially all that the fossil record offers to help in species recognition, what is he or she to do?

The only reasonable yardstick is to look not so much at the variation that accumulates *within* species (for all species will be variable, and in closely related species ranges of variation will be likely to overlap pretty much totally in most characteristics), but at the kind of variation you typically find *among* closely related species. This latter, as we've seen, is precisely the kind of thing paleoanthropologists have not been accustomed to doing much of. And when they do turn their attention beyond *Homo sapiens*, they traditionally focus on our closest living relatives, the apes. After all, as our nearest kin, the apes surely have the most to tell us about ourselves. There are two problems with this, however. One is that the great apes, while undeniably our closest *living* relatives, are not actually all that close: for while most other living primate species have relatives within their own genus, the apes lie well outside ours. More significantly, though, today's great apes, members of a group that has been steadily declining since the later Miocene, are not very diverse at all. There's a big debate going on right now about exactly how many species there are of great apes, but it's unlikely that any of the four genera has more than two. In this instance nature, not history, has conspired to diminish diversity as a factor in the paleoanthropological consciousness; the result, however, is much the same.

But if you step back a little and look at the patterns of morphological distinction among primates that have a little more species diversity, you notice one thing very clearly: certainly as far as bones and teeth are concerned, closely related species (those belonging to the same genus—*Homo*, perhaps?) do not typically differ very much. As I've noted, it's at the level of the genus that you routinely pick up clearly recognizable differences. Most of the time (not necessarily invariably, though) you will have to look pretty closely at the bones and teeth to discriminate consistently between members of two species belonging to the same genus—and even then you often cannot be sure. This in turn means that looking in the fossil record for infraspecific taxa—namely, the subspecies beloved of paleoanthropologists—is a totally futile pursuit. In contrast, however, when you find yourself comparing fossils that fall into two recognizably distinct "morphs," you can be pretty certain that you have (at least) two species in your sample.

This realization, born of years of studying the diversity of the lemurs (the "lower" primates of Madagascar), made conventional interpretations of species diversity in the human fossil record look a little odd to me. Oddest of all in the mid-1980s was the way in which most paleoanthropologists divided up the fossils representing the most recent half-million years or so of human evolution. Everything from this period (except for a few late *Homo erectus*

stragglers such as those from Ngandong) was classified in *Homo sapiens*. Yet there was a very large amount of morphological variety among these fossils; and this variety was well enough compartmentalized for at least three informal names to be in common use for different groups of them: Neanderthals (a.k.a. *Homo sapiens neanderthalensis*), “archaic *Homo sapiens*” (just about everything else that didn’t happen to look exactly like us), and “anatomically modern *Homo sapiens*.” Well, if various groups of fossils are distinct enough to be routinely identified by name, you can be pretty sure that you have at least as many species as you have names. I suggested this in a paper published in 1986, and, while I can hardly claim that my contribution revolutionized paleoanthropology, I think it was at least symptomatic of a trend that has recently gathered some steam. Specifically I urged that, at the very least, the Neanderthals be restored to separate species status as *Homo neanderthalensis*. Similarly, the Arago, Petralona, Bodo, and Kabwe fossils (and probably also Dali and Jinniushan) should be classified together with others like them in their own species. If the Mauer jaw belongs to this group (as we can reasonably assume on the basis of the resemblances between the Mauer and Arago jaws) we can call this one *Homo heidelbergensis*. Most emphatically of all, I stressed that our own living species, *Homo sapiens*, is as distinctive an entity as exists on the face of the Earth, and should be dignified as such instead of being adulterated with every reasonably large-brained hominid fossil that happened to come along.

I pointed out also that the later part of the Pleistocene had been a period of extreme fluctuation in climate. Vegetation zones had moved north and south, up-mountain and down. Extensive woodlands had been fragmented by invading steppe or savannas and had been rejoined as forests returned. Glaciers and harsh periglacial climates had made vast areas of northern Eurasia periodically uninhabitable by hominids, presumably spurring major migrations and causing local extinctions. Sea levels had risen and fallen, alternately creating islands and producing land bridges. Perhaps no period in the history of the globe had been more conducive to the emergence of new species and to competition between related species newly in contact: in other words, to what we perceive in hindsight as macroevolutionary change. And the variety seen among later Pleistocene hominid fossils was, in fact, exactly the kind of thing one might expect to find under these conditions.

A Single Origin

An origin of *Homo sapiens* through normal processes of allopatric speciation implies that, far from being a worldwide phenomenon, this origin was associated with a particular area of the world. And, even as the multiregional continuity bandwagon gathered momentum, an alternative scenario was beginning to be aired. Eventually becoming familiar as the “Out of Africa” hypothesis of modern human origins, the basic notion was that *Homo sapiens*

arose somewhere in Africa at a relatively recent date. Subsequently, mimicking *Homo ergaster*, these ancestral modern people spread out from that continent to colonize all the habitable parts of the Old World—and eventually, of course, of the New World too. The crucial difference was that, while ancient *Homo* had dispersed from Africa into virgin territory, the early *Homo sapiens* had moved into regions already occupied by hominid relatives, which, necessarily, were displaced in the process. An early proponent of one version of this viewpoint was the University of Hamburg's Günter Bräuer, who in several papers published in the mid-1980s pointed out that, sparse as the relevant fossil record was, the earliest evidence for modern human anatomy came from eastern and southern Africa. Bräuer saw the migrant Africans as having displaced the Neanderthals in Europe, but he was unsure about what had happened in the Far East. And though others, such as Chris Stringer of the (then) British Museum (Natural History) were less reticent in generalizing the "Out of Africa" scenario to embrace the Old World as a whole, what really catapulted it into the limelight was a series of genetic studies done in the laboratory of Allan Wilson at the University of California, Berkeley.

Wilson and his colleagues had actually revived an approach originally initiated in the mid-1970s by a couple of geneticists, Masatoshi Nei and Arun Roychoudhury, but which had not attracted much attention at the time. Nei and Roychoudhury had looked at blood proteins in members of human populations in Europe, Africa, and Asia. They had found that interpopulation differences were rather small compared to those found within populations, but that the net differences between Africans and both other groups were significantly larger than those between Europeans and Asians. This, they concluded, meant that Europeans and Asians shared a common ancestry more recently than either did with Africans, and they calculated that the split between Africans and Eurasians had taken place about 115–120 kyr ago, while the European–Asian divergence was only about 55 kyr old. Wilson and his students Rebecca Cann and Mark Stoneking took this approach farther, specifically by examining mitochondrial DNA (mtDNA).

The Mighty Mitochondrion

DNA is, of course, the long-stranded molecule that carries the genetic instructions from which each new individual is built. Most DNA resides in the nucleus of the cell, and in sexually reproducing species each individual's nuclear DNA is inherited in more or less equal proportions from each parent. However, a small amount of DNA is also contained within tiny distinct structures in the cytoplasm of the cell known as mitochondria; and what is particularly interesting about mtDNA is that it is inherited only from the mother (whose ova are entire cells, whereas the father's sperm contains only nuclear DNA). Thus, while nuclear DNA is jumbled up in each new generation, mtDNA passes from mother to child pretty much unscathed—theoretically, in an unbroken

sequence stretching back to the ancestral "Eve." Unscathed, that is, except for any mutations that may occur along the way. And in mtDNA mutations appear to accumulate at many times the rate typical of nuclear DNA, perhaps because they are not affected by natural selection in the way in which many changes in nuclear DNA are.

From the first, studies of human mtDNA showed a remarkable uniformity within the species. And since diversity is expected to increase with time, this uniformity suggested a relatively recent origin for *Homo sapiens*. By assuming an average rate of change of about 3% per million years, Wilson and his colleagues initially came up with a molecular time to origin for *Homo sapiens* of about 400 kyr. This would have placed the ancestress of modern humanity late in the time span of *Homo erectus*, though this was still hardly congenial to the multiregional continuity crowd, whose perspective stretched back over twice that far. It was, however, also at odds with what the fossil record told us about the earliest appearance of modern human anatomy, and energetic debate ensued. Within a short time Wilson and his collaborators reduced the age of "Eve" to about 200 kyr, and following Wilson's premature death in 1990, Mark Stoneking recalibrated this date to about 140–130 kyr—which fit well with the dates from Klasies River Mouth and elsewhere. Recently the molecular time to origin has crept back a bit once more—as have the paleontological indicators, of which more later.

Molecular dates, which depend on a lot of assumptions, will always be argued over. More significantly, though, African mtDNA, just like Nei and Roychoudhury's proteins, turned out to show considerably more diversity—i.e., a greater accumulation of mutations—than was found in the mtDNA of Europeans, Asians, and Australasians. Since mtDNA diversity is in some way a function of time, it followed that the African population had been evolving for the longest since the genetic bottleneck at its origin; the less diverse populations split off more recently. "Eve," in other words, was African. Further, the rather homogeneous nature of human mtDNA (and thus a relatively recent origin for *Homo sapiens*) was rapidly confirmed (comparative studies showed that as much mtDNA variation could be found among local populations of chimpanzees as among the entire modern human population); most significantly of all, the mtDNA data did appear to agree with what the admittedly less-than-perfect fossil record also appeared to be telling us.

Refinements in Dating

The debate between the apostles of the Multiregional and "Out of Africa" scenarios was just beginning to attract the kind of media attention formerly associated with the Leakey/Johanson brouhaha, when new dating methods began to make the fossil picture of the origin of *Homo sapiens* more suggestive yet. The time gap between the effective ranges of radiocarbon dating and K/Ar and similar techniques had left a very significant period of human

evolution without any means of radiometric calibration. The 1980s saw the introduction or refinement of a number of new dating technologies that helped to fill this gap. Three of them, at least, deserve special mention here: electron spin resonance (ESR), thermoluminescence (TL), and uranium-series (U-series) dating.

Electron spin resonance dating, proposed as early as 1967 but only in practical application since 1975, depends on the fact that bombardment of crystalline materials by natural radiation leads to the trapping of free electrons in defects in the crystal lattice. The rate of trapping is determined by the level of background radiation. The energy of the trapped electrons can be measured and a date derived from the ratio between this figure and the trapping rate, which is in turn derived from measurement of the background radiation (the "external dose") plus radiation from unstable isotopes absorbed by the fossil itself (the "internal dose"). The background rate can vary from one place to another, and even within the same site. So even though the electron spin resonance technique can be used directly on substances such as the dental enamel of fossils themselves (currently the material of choice), or on contemporaneously formed materials such as calcite, there must be enough of the initial archaeological or geological deposit left to allow accurate measurement of the background radiation. With older sites this is not always the case, and in such instances accurate dates can't be obtained. The internal dose depends on the rate of uptake of radioactive isotopes by the fossil; this cannot be measured directly, but the date can usually be bracketed by certain limiting assumptions. There are a number of additional complications that narrow the range of potentially datable materials and deposits, but even as early as the 1980s the reliability of dates obtained by electron spin resonance was rapidly improving, and the technique holds great promise for the future, as well as surprises in the present.

Thermoluminescence dating, in use since the 1980s, is based on similar principles to ESR, but the trapped electrons are measured in a different way. Again, the idea is to measure the number of electrons that have become trapped in the crystal lattice of a mineral. When a mineral is formed all of the traps are empty, but at that point they began to fill up at a regular rate, again determined by background radiation and other specifiable factors. Archaeologists, however, are not interested in when a mineral was formed; they want to know when it was that humans used it. Heating and certain other processes empty the electron traps and thus reset the clock to zero; this is why flints burned in campfires have become popular objects for dating, as, for more recent periods, have bits of pottery. Even exposure to sunlight can have reset some small objects; thus, under certain conditions various kinds of artifact- or fossil-enclosing sediments can also be dated. The actual dating is done by heating the specimen once more and measuring the intensity of light given off as the trapped electrons are released. If you know the background radiation that stimulated the filling of the traps, plus the sensitivity to

radiation of the material itself (which can be determined experimentally), you can then calculate the date at which your flint was heated or when the sand grains around your artifacts lay upon the surface.

Uranium-series dating relies on a different principle. Unstable uranium atoms decay at characteristic rates to various different daughter products. The daughter product most favored by archaeologists is thorium-230 (^{230}T), and the preferred materials for dating are freshwater-deposited limestones such as stalactites and travertines. Normally the radioactivity of ^{230}T in an undisturbed material will be equivalent to that of the parent uranium in the sample. However, this equilibrium will not obtain in newly formed limestones. Since uranium is soluble in the water that deposits these limestones, while thorium is not, the newly forming stalactite will contain uranium but no thorium. At that point the ratio of thorium to uranium in the stalactite will be zero, but as time passes more thorium will accumulate in it as uranium decays to thorium. The age of the stalactite can thus be estimated from the size of this enlarging ratio. Techniques for measuring the isotopes of uranium and thorium are improving and, along with them, the accuracy of this method of dating. The particular attraction of U-series dating is that many archaeological sites are in caves in limestone regions. Datable travertines, flowstones, stalactites, and so forth are, of course, common in such places. And, at least potentially, other calcium-containing structures such as bones, teeth, and mollusc shells are also datable using this technique.

Levantine Coexistence

These and other new dating methods had a major impact on our understanding of the emergence of *Homo sapiens* and of the period during which *Homo sapiens* and *Homo neanderthalensis* coexisted. U-series and ESR dates have, for example, combined to confirm the great antiquity (over 90 kyr) of the Middle Stone Age modern humans from Klasies River Mouth, in South Africa; they also suggested that the Border Cave moderns were in excess of 75 kyr old. But the real surprises came from sites in the Mediterranean basin. ESR dates on mammal teeth from the same levels as the human burials at Skhül and Tabün have come out at about 100 and 120 kyr, respectively. You'll recall that the former have been widely seen as anatomically modern, or so close to it as to make no difference, while the latter were always seen as Neanderthal. Both dates were much more ancient than anyone had expected, and this confirmed that in the Levant Neanderthals and moderns had coexisted in some fashion at a very early date. The exact nature of that coexistence remained unclear. It was possible that the two hominid species lived cheek-by-jowl (Tabün is a leisurely five-minute stroll from Skhül), though intuitively this seemed unlikely; more plausible is that the two species occupied the area alternately, maybe as the local climate fluctuated. But, whatever the case, coexistence was a long-term phenomenon, for Neanderthals lingered in the region undiluted until at



Side and front views of the ancient anatomically modern human cranium Qafzeh 9, from Jebel Qafzeh, Israel. Scales are 1 cm. *DM*.

least about 50 kyr ago, based on a very recent ESR date from Kebara. TL dates on burned flints from Jebel Qafzeh, where at least some of the human remains are modern by anybody's standards, confirm this lengthy overlap by revealing an antiquity of over 90 kyr. And, on the African side of the Mediterranean, the supposedly modernish skulls from Jebel Irhoud were dated by ESR at possibly over 100 kyr.

This was very different from the traditional picture formed on the basis of western European evidence. There, the story was more clearly one of abrupt replacement of the Neanderthals by modern types (although as later dates for Neanderthals came in from Iberia, and as recalibration of radiocarbon dates pushed back the dates of early modern occupation of Europe, clarity appeared to diminish a little). What I found particularly interesting, though, was that it was at just about the time of the latest Neanderthal fossil (not, of course, the same thing as the last Neanderthal) known from the Levant that the first evidence of Upper Paleolithic industries in the region showed up. In Europe such industries were and are associated with undisputed moderns, and, although the very earliest Levantine Upper Paleolithic (from the 45 kyr site of Boker Tachtit, in the Negev desert) was not associated with human fossils, it was not unreasonable to believe that anatomically modern humans (who had, after all, been around in the area for 50 kyr) were responsible for it. Can we then say that Neanderthals disappeared from the area when *Homo sapiens* stopped merely looking modern and began to behave in a modern fashion as well? I'd still personally bet that we can, but until we have more and more precisely dated archaeological sites and hominid fossils from this time and place, we won't be sure.

The subject of behavior was complicated by the fact that, while in Europe Upper Paleolithic stone and bone tools were associated from the beginning

with evidence of "creativity" in the form of engravings, sculpture, notation, musical instruments, and so forth, this was not the case in the Levant. What's more, the earliest Upper Paleolithic tools from Boker Tachtit, while fully Upper Paleolithic in concept, were made using techniques that had been current in the Middle Paleolithic. However, since anatomically modern humans had apparently made Middle Paleolithic tools for the first 50 kyr of their existence, we probably shouldn't find this too surprising.

If the Neanderthals and moderns had shared a substantial bit of the world over an extended period of time, it is vanishingly improbable that there was no interaction between them. And if interaction there was, what was its nature? One school of thought, in which the advocates of regional continuity figured prominently, found evidence of hybridization in variable morphologies among Neanderthals and moderns. To them, the distinctive Neanderthal morphology was eventually "swamped" by the genes of the incoming moderns through interbreeding. A number of factors argued against this, however. The first of these was that evidence of "hybrid" fossils (or fossils that could be convincingly interpreted as such) was poorest in just that region of the world where evidence for long-term cohabitation was best. Another was that, if the Neanderthals were a separate species from ourselves—which the continuity people denied, of course—significant interchange of genes would not have been possible (though, possibly, individuals might willingly or unwillingly have participated in attempts to hybridize). And yet another came from observation of the generally nasty ways in which invading modern peoples have tended to treat each other—let alone other species—throughout recorded history. The idea of a gigantic late Pleistocene love-in among morphologically differentiated hominids simply defied every criterion of plausibility. There were other reasons, too. For example, if Lewis Binford was right about Neanderthal behavior, the incompatibility in behavioral systems between Neanderthals and moderns contemporaneous with them would make successful intermixing highly implausible. But the real lesson of all this debate during the 1980s and 1990s—and it is an enduring lesson—was that both the fossil and the archaeological evidence needed to be passed through a powerful filter of perception before it was possible to swallow the conclusion either that Neanderthals were our forebears, or that those forebears somehow incorporated the Neanderthal gene pool into their own.

CHAPTER 17

Another Fin de Siècle

Paleoanthropology is always full of the unexpected, and the decades around the turn of the second millennium were no exception, as the redating of the Qafzeh hominids proved early on. Among many other surprises was the discovery, announced in 1997 by the archaeologist Hartmut Thieme, of several long and carefully shaped wooden spears at a northern German site called Schoeningen. There is little doubt that wood must have been exploited by hominids since as far back as the technology was available to cut it, but it is only rarely preserved beyond a few centuries, and the oldest wooden implement known up until Thieme's 400-kyr-old discovery was a broken-off spear tip found lodged between the ribs of a 125-kyr-old straight-tusked elephant at Lehringen, also in Germany. It had been assumed that the Lehringen artifact was the remains of a thrusting spear that must have been wielded close-up to its target; but the perfectly preserved Schoeningen implements, between six and seven feet long, were clearly shaped to the form of a modern throwing spear, with the center of balance toward the front. The tip was sharpened to a fine point, and Thieme interpreted these missiles as the oldest complete hunting weapons yet discovered.

The Stony Brook University archaeologist John Shea has pointed out that, absent a stone tip, the penetrating power of these missiles would have been limited; but at the very least these artifacts give us pause about the notion that sophisticated hunting techniques only appeared later, along with *Homo sapiens*. If these truly were throwing spears, their makers could have hurled their missiles from a safe distance, rather than having to confront their doubtless unfriendly prey up close as they would have had to do if all they had was thrusting weapons. All in all, there is a strong suggestion here that technologies, and the behaviors inferred from them, may have been somewhat more sophisticated than was inferred from the form of the stone tools alone. This suggestion is enhanced by the fact that in recent years evidence has been found, in the form of traces of mastic still adhering to them, that some Middle Paleolithic stone tools were hafted to create complex implements. We don't

know exactly what they were hafted into, but depending on the form of the stone tools involved, both handles and spear ends are likely.

Diet and Isotopes

The 400-kyr-old Schoeningen spears were made at a period during which several other seminal technological innovations were showing up for the first time in the hominid record—recall Terra Amata and Bilzingsleben, for example. The identity(ies) of the hominid(s) who made these advances is debatable, but it was certainly not *Homo neanderthalensis*, which had yet to make its appearance. Still, if these technologies were available to Neanderthal precursors, they were almost certainly available to the Neanderthals themselves, and substantiation of the corollary that these hominids were sophisticated hunters was also beginning to emerge from an entirely new avenue of inquiry that became available only in the last couple of decades of the twentieth century.

This new approach is based on the proposition that “you are what you eat,” and it involves the measurement of the ratios between various isotopes present in any collagen that might be preserved in fossil bones. As we saw earlier, unstable isotopes of certain elements that decay at regular rates were important in developing the first chronometric dating methods; in dietary studies it is the stable isotopes that are looked at, particularly those of nitrogen, oxygen, and carbon. In the case of the Neanderthals the favored isotopes are of nitrogen. The ratio between the isotopes ^{15}N and ^{14}N is known to increase by about 3‰ with every step up the food chain: the higher the ratio, the more meat that is eaten. In 1991, a group led by the French paleobiologist Hervé Bocherens published the first results of a nitrogen isotope analysis of Neanderthal teeth and bones from the site of Marillac in France. Not only did this study demonstrate that chemically intact collagen could indeed be recovered from hominid bones over 40 kyr old, but the signal obtained was one of carnivory; and a string of studies over the next decade or so confirmed this at site after site: the Neanderthals always came out with much higher $^{15}\text{N}/^{14}\text{N}$ ratios than the herbivores at each locality, and were instead comparable to (or even higher than) the wolves, lions, and hyenas.

Eventually, Neanderthal samples spanning a period of many tens of thousands of years were found fairly consistently to give the isotopic signature of a top predator in an open steppe environment. But Bocherens and his collaborators went further yet: on the basis of a very high ratio derived from the St-Césaire Neanderthal skeleton (higher than those obtained from hyenas at the same site), they suggested in 2005 that the Neanderthals at St-Césaire had specialized in consuming herbivores that were themselves particularly high in ^{15}N —namely, mammoths and woolly rhinoceros! What’s more, they suggested that such a high proportion of these large, fearsome animals in the diet could not have simply been scavenged; at least a substantial number must

have been actively hunted, presumably as part of a longstanding tradition of dietary specialization.

Isotopic data on the Neanderthals and the penecontemporaneous Cro-Magnons are still coming in, and there is some argument over what, exactly, these data mean; it has been suggested, for example, that there may be some physiological, rather than dietary, reason, for the Neanderthals' elevated ^{15}N . But there is no doubt that these studies have changed our perspective on *Homo neanderthalensis*. Clearly, these hominids were a lot more than predators on small game and opportunistic scavengers of larger carcasses: they were capable hunters of large-bodied mammals who were, moreover, able to adapt with some facility to changing circumstances. The archaeologists Mary Stiner and Steven Kuhn, for example, showed that Neanderthals at neighboring cave sites in Italy that dated from the last interglacial, about 120,000 years ago, and from the last glacial, some 50,000 years ago, showed evidence of very different strategies for dealing with what were very different environments at the different times.

The archaeologists Bryan Hockett and Jonathan Haws remarked in 2003 that "diverse diets seem to have been a trademark of humans in lower and mid-latitudes during the late Pleistocene," and such diversity of diet presumably reflected the wide range of resources typically available in the tropical to subtropical zones in which *Homo sapiens* is thought to have evolved. In the Neanderthals' colder northern heartland, in contrast, the array of available foods during the later Pleistocene seems to have been considerably narrower than in the tropics, and the most obvious dietary resource available to any hominid in this region was the proteins and fats offered by the vast herds of grazing animals that teemed on the Ice Age European steppes. Nonetheless, over the long history of the Neanderthals, environments and resources certainly did not remain uniform in place or in time, and these hominids showed a remarkable flexibility in responding to prevailing conditions. In the words of Harvard's Ofer Bar-Yosef, the Neanderthals almost certainly "ate what was there."

Neanderthal Environmental Preferences

Significantly, though, the Neanderthals seemed to have avoided extremely severe environments. In 2006 the French anthropologist Marylène Patou-Mathis reviewed the evidence and found that Neanderthals tended to avoid periglacial environments. She pointed out that at the end of the penultimate glacial, Neanderthals were limited to central and western Europe, only expanding eastward during the kinder conditions of the last interglacial. In particularly cold subsequent periods Neanderthals avoided periglacial areas in favor of more temperate microclimates, entirely deserting the frigid central European plains. A similar pattern over Oxygen Isotope Stage (OIS) 3 (ca. 60–20 kyr) was perceived in 2004 by the biologist Clive Finlayson and

by the contributors to a volume edited in 2003 by the geologist Tjeerd van Andel and William Davies, who found that Mousterian peoples, limited to the southern fringes of Europe at 70–60 kyr, expanded eastward and northward during the warmest phases of OIS 3, but subsequently contracted toward the south as climates cooled again.

Such observations were bound to call into question the traditional assumption that the Neanderthals were “cold-adapted,” in contrast to our own “tropically derived” species. Originally this assumption was based on body proportions. In Neanderthals these were claimed to follow Bergmann’s and Allen’s Rules, whereby animals in colder climates are expected to have greater body mass and shorter extremities. Wide bi-iliac breadth and great trunk widths were claimed as evidence of high body mass in Neanderthals, as they appear to be in some Eskimos, while limb indices were described as Eskimolike. However, as we will see shortly, flaring ilia and wide-based thoracic cages are primitive for the wider hominid radiation to which the Neanderthals belong (and possibly also for *Homo* in general), and thus can hardly be viewed as adaptations to the specific environmental conditions encountered by the Neanderthals as the last-surviving species of that radiation. As to limb indices, a review by the University of New Mexico’s Osbjorn Pearson and colleagues in 2006 “de-emphasize[s] the distinctiveness of Neanderthals.” Furthermore, John Stewart of University College London convincingly argued that if *Homo neanderthalensis* and *Homo sapiens* were indeed different species, any differences in limb segment proportions would not, in any event, necessarily imply the implementation by Nature of Allen’s Rule. Indeed, Stewart went so far as to suggest, in tune with with Finlayson, that Neanderthals were “interglacial survivors” who became extinct simply as part of a larger faunal turnover that occurred as the Last Glacial maximum approached. Attacking the question from yet another angle, in 2003 the paleoanthropologist Leslie Aiello and the physiologist Pete Wheeler concluded, on anatomical and physiological grounds, not only that Neanderthals could not have survived in many of the areas they are known to have occupied without considerable cultural accommodation, but that they had at best possessed only a “modest advantage over Anatomically Modern Humans in their lower critical and minimum sustainable temperatures.”

The logical inference from all this—that Neanderthals were not fine-tuned biologically (or indeed culturally) to conditions of severe cold—is supported by what is known about Neanderthal distributions in time and space. This indicates that, although they inhabited a continent that offered sub-Arctic to Arctic conditions in addition to temperate ones, they preferentially sought out the more temperate areas available to them. Significantly, this pattern contrasts strikingly with the evidently rapid expansion northward in the later phases of OIS 3 of the newly arrived and “tropically derived” *Homo sapiens*. These modern people, unquestionably aided by an unprecedented capacity for cultural accommodation, had swiftly pushed northward to establish themselves above

the Arctic Circle in Siberia by around 27 kyr, in the immediate run-up to the last glacial maximum.

The Neanderthal Body

Our emerging picture of the Neanderthals is, then, of a very capable hominid species that was able to adapt behaviorally to a wide variety of environmental circumstances even as it wisely avoided extremes. But being smart and adaptable doesn't necessarily mean being just like *Homo sapiens*. Their lack of "cold-adapted" body proportions notwithstanding, it had long been known that, besides their marked distinctions in skull structure, the Neanderthals differed from us in numerous details of the postcranial skeleton. Such differences included the thickness of the long bones, the expansiveness of the articular ends of those bones, the broad pelvis with its characteristically long, thin pubic bone, the strongly-ridged finger bones, and a host of other features. As a result, after their restoration in the 1960s to full straight-kneed uprightness, Neanderthals were still routinely depicted as squat and hugely muscled versions of *ourselves*.

Still, while in the 150 years following the Feldhofer discovery several associated Neanderthal skeletons had been found, not one of them was anywhere near complete enough to have motivated anyone to make a complete restoration of a full Neanderthal skeleton. Eventually, in 2001 the Dolan DNA Learning Center asked Gary Sawyer and Blaine Maley of the American Museum of Natural History to make such a restoration, which could only be done by combining elements from several different Neanderthal skeletons. Fortunately, the La Ferrassie 1 skeleton was sufficiently complete that, on one side of the body or the other, there was a continuous representation of elements from head to toe; this guaranteed the reliability of the overall limb proportions of the composite. The resulting skeleton, incorporating elements of seven different individuals from as many sites in six countries, was a revelation.

Here was a creature that would have looked very different on the landscape from any modern human being, as the accompanying illustration shows. Modern humans have a very distinctive torso. Their barrel-shaped rib cage, lying high above a narrow pelvis, tapers inward both at its top and at its bottom. In contrast, the Neanderthal thorax broadens dramatically outward, from a narrow top, to match the wide, flaring pelvis below. What's more, the articulation of the spine with the back of the pelvic bowl lies low down, shortening the waist: not only would this Neanderthal have looked very different from a Cro-Magnon, but his gait would have been very different. This was something that the Israeli paleoanthropologist Yoel Rak had already suggested back in the 1980s after studying the Neanderthal pelvis; in 2003 the conclusion was independently reinforced by Fred Spoor and colleagues, who found that the semicircular canals of the Neanderthal inner ear, already known to be



Composite reconstruction of a complete Neanderthal skeleton (left), compared with a *Homo sapiens* of similar stature. Photo by Ken Mowbray.

uniquely configured, “may reflect a pattern of head movement different from modern humans, possibly related to aspects of locomotor behaviour.”

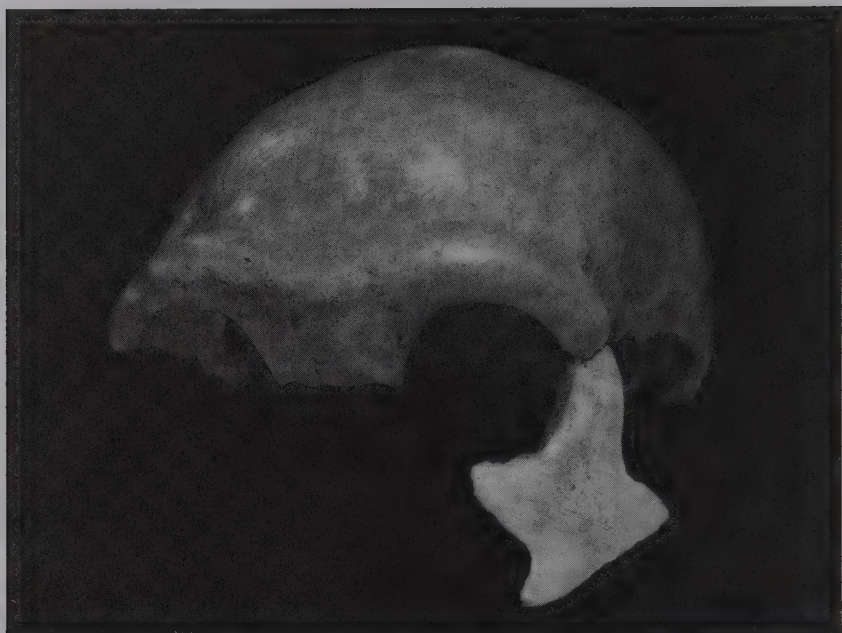
The Sawyer/Maley Neanderthal reconstruction thus added heft to the already weighty argument that these hominids should be dignified as their own species, *Homo neanderthalensis*. For it certainly reduces the likelihood that Neanderthals and modern humans would have recognized one another as natural mating partners. There are no silver bullets in fossil species recognition, though, and any judgment on this matter naturally involves weighing as many considerations as possible.

One other factor that might bear on this question was the matter of how long young Neanderthals took to develop. As we have seen, modern humans are remarkable for their prolonged growth period and differ in this from early members of the genus *Homo* in whom the growing—and presumably learning—interval was much shorter. In 2004, just before Sawyer and Maley published their reconstruction, the European paleoanthropologists Fernando Ramirez-Rozzi and Jose Maria Bermúdez de Castro published a study showing that Neanderthal teeth developed significantly more quickly than human ones. They thus concluded that the Neanderthals had a relatively short growth and learning period—which excluded them from *Homo sapiens*. However, in the following year another group led by Chris Dean found that Neanderthals in fact fell within the envelope of modern human variation in this respect; and in 2006 Roberto Macchiarelli and colleagues used new methods of visualizing the internal microstructure of teeth to conclude much the same. But in 2007 the pendulum shifted back toward rapid growth with early cessation when Tanya Smith and colleagues reported on teeth from a juvenile Neanderthal unearthed at the Belgian site of Spy.

Still, while the case might not yet be conclusively demonstrated from teeth that *Homo neanderthalensis* and *Homo sapiens* differ significantly in the timing of growth, Marcia Ponce de Leon and Christoph Zollikofer of the University of Zurich showed in 2001 not only that the faces of the two hominids exhibit entirely different growth trajectories, but that some particularly characteristic Neanderthal features are evident from very early indeed in the development of the individual. This by itself implied a long period of evolutionary separation between *Homo neanderthalensis* and *H. sapiens*. The distinctiveness of juvenile Neanderthal morphology was also dramatized during the 1990s by the discovery by a Japanese–Syrian group of two amazingly well-preserved infant skeletons at the Syrian site of Dederiyeh, the recovery of another at Amud in Israel, and the remarkable rediscovery in 1996 by Bruno Maureille of a neonatal Neanderthal skeleton from the key site of Le Moustier that had been missing for almost 90 years.

DNA from Neanderthals

The notion that Neanderthals were profoundly different from *Homo sapiens* also received a boost from the first successful attempt to obtain mtDNA from a hominid fossil. This extraordinary feat was pulled off in 1997 by a team led by the molecular systematist Svante Pääbo, then of the University of Munich and now at the Max Planck Institute for Evolutionary Anthropology in Leipzig. The fossil from which the DNA was extracted was the original Feldhofer Neanderthal individual. As you will recall, this specimen came from a site that was subsequently completely destroyed by the workmen who found it. Let me add here that—amazingly—150 years later the paleoanthropologist Ralf Schmitz and the archaeologist Jürgen Thissen figured out where



Three-quarter view of the original Feldhofer Neanderthal skullcap, with the newly discovered cheekbone attached. *Photo by Sara Arias.*

the debris from the cave had been dumped by the miners, and retrieved more hominid fragments from the dump. These included a cheekbone that articulated with the original skullcap, and part of the skeleton of a second individual. Direct dating by AMS radiocarbon had already yielded an age of about 40 kyr for the original skeleton, pretty much in line with expectation, and now the molecular findings on the same specimen also corroborated the expectations of those who believed that Neanderthals and modern humans belonged to different species. For when a short stretch (360 bp) of the Neanderthaler's mitochondrial genome had been isolated, it proved to fall entirely outside the range of variation seen among modern humans.

To be exact, the study found that while the average number of differences among modern humans in this part of the mitochondrial genome was eight, and that between humans and chimpanzees was about 55, the human-Neanderthal difference was 26. What's more, the Neanderthal mtDNA was more or less equidistant from that of all modern *Homo sapiens* populations, lending added weight to the suggestion that the two lineages had evolved separately for an extended period. Since 1997, mtDNA has been obtained from a dozen more Neanderthals from sites in central and eastern as well as western Europe. These studies showed that the Neanderthals differed among themselves in their mtDNA sequences just as we do, but still remained substantially outside the modern human envelope. Differences between us and them

are typically three times greater than those found between the most distant modern human populations. Remarkably, one such study even extended the geographical range of *Homo neanderthalensis* some 1200 miles to the east: in 2007 Johannes Krause and colleagues used DNA analysis to determine that otherwise unidentifiable bone fragments from Oladnikov Cave, in the Altai Mountains of Siberia, were in fact Neanderthal.

In addition to all this, no "Neanderthal" mtDNA sequences were found in extensive studies of modern European populations, and studies of Cro-Magnon samples have similarly failed to reveal any evidence of Neanderthal admixture. It has been argued that Neanderthal genotypes might have been lost from later European populations through genetic drift, but in 2003 an Italian-led group found that no Neanderthal influence could be found in the DNA of 24-kyr-old *Homo sapiens* from the cave of Paglicci, in southern Italy. There has long been some concern about the possibility of contamination of ancient *Homo sapiens* samples by modern human DNA derived from the laboratory, but this study was carefully conducted and was also supported by similar results on Cro-Magnon fossils from another Italian site.

What is more, in 2004 the Swiss geneticists Mathias Currat and Laurent Excoffier mathematically modeled the range expansion of modern humans into Europe and their potential admixture with Neanderthals and found that on present evidence any potential interbreeding rates would have been smaller than 0.1 percent. This tiny number is effectively zero, and to Currat and Excoffier it "strongly suggests complete sterility between Neanderthal females and modern human males, implying that the two populations were probably distinct biological species."

Interestingly, in 2006 a group led by the University of Chicago molecular geneticist Bruce Lahn reported discovering a version of the microcephalin gene that had apparently been incorporated into the human population only some 37 kyr ago, yet that was so different from other versions of the gene in humans that the authors felt it must have been incorporated from some other hominid lineage. This implied that early *Homo sapiens* had interbred with some other lineage, but although Lahn and colleagues mentioned Neanderthals as a possible candidate for this lineage, they really only did so because Neanderthals were around at the time and they happened to have heard of them.

Hybrid Red Herrings

Still, suggestions of Neanderthal-modern intermixture refuse to go away, and presumably never will. One of the most highly publicized recent suggestions to this effect was made in 1999 by the Portuguese archaeologist Cidalia Duarte and colleagues in announcing the discovery of a child's skeleton in the rock shelter of Lagar Velho in Portugal's Lapedo Valley. The skeleton had been interred some 24.5 kyr ago in what was in most respects a typical Gravettian burial. However, the skeleton itself was claimed to show "a mosaic

of European early modern human and Neanderthal features." On closer inspection most of the claimed Neanderthal features proved to be without much substance (full disclosure: my colleague Jeffrey Schwartz and I were extensively and personally vilified by the authors when we very discreetly pointed this out in a commentary that accompanied their article), and the publication of a very handsome monograph on the Lagar Velho specimen, which after all had lived around 4 kyr (about 200 generations) or more after the last bone fide Neanderthals had disappeared, did not provide material grounds for altering that conclusion. Sadly, the specimen contained no undegraded DNA, and although new techniques may of course become available in the future to reopen the issue, it is probably fair to say that most paleoanthropologists are at most maintaining the Lagar Velho child in a "suspense account."

The most notable subsequent claim for paleoanthropological evidence of Neanderthal-early modern admixture came from Romania, whence, in collaboration with local colleagues, the American paleoanthropologist Erik Trinkaus (one of the Lagar Velho team) described newly discovered modern human fossils from the site of Peștera cu Oase ("Cave with Bones") in the southwestern Carpathians. Aurignacian (early Upper Paleolithic) skeletons are few and far between, and are thus of the greatest interest; and the first find from the Peștera, announced in 2003, was an adult modern human mandible directly dated by AMS radiocarbon to about 35 kyr ago (in reality the specimen is probably older, since recent recalibration of the radiocarbon scale suggests that in this general period actual calendar dates are a bit older than their radiocarbon equivalents). This date makes the fossil very early in the first wave of human penetration of Europe, and it was certainly contemporary in the region with the resident Neanderthals. Inevitably, then, the specimen was going to be intensively scrutinized for "Neanderthal" features, and one (very minor) candidate feature was found, transforming the specimen into a modern/Neanderthal "mosaic." In 2007 a largely complete cranium of a late adolescent, believed to be about the same age, was described from the same site. Again, there is nothing about this *Homo sapiens* specimen that would convincingly suggest any Neanderthal admixture, but its describers nonetheless concluded that it was somehow "nonmodern," indicating "complex population dynamics as modern humans dispersed into Europe."

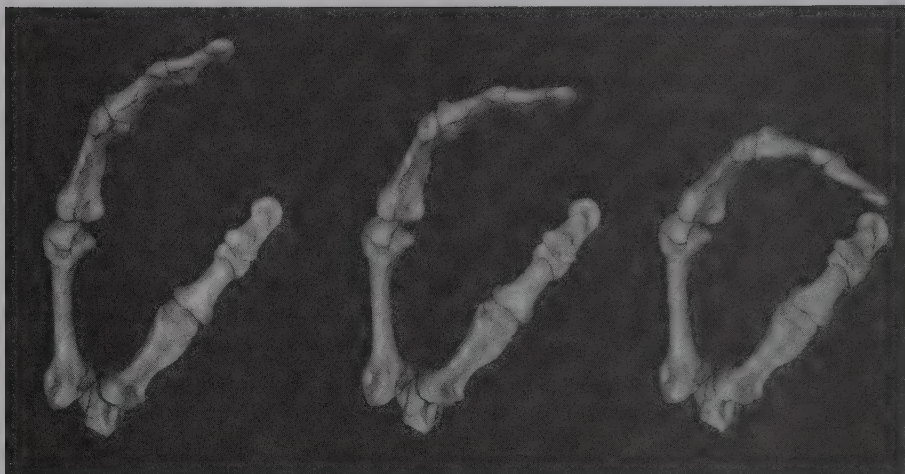
Whatever exactly this meant, it echoed a conclusion some of the same researchers had arrived at the year before on the basis of 30-kyr-old *Homo sapiens* remains recovered in the 1950s. These had been found a bit to the northeast, at the Peștera Muierii ("Cave of the Old Woman"); again, in the one cranium available, the group found a few "Neanderthal" features among an overwhelming preponderance of *Homo sapiens* characteristics. First among these are a "moderately low frontal arc" and an "occipital bun." Yet even a brief glance at the illustration of the cranium shows that there is nothing about the form of either the forehead or of the occipital curve that cannot be much more easily matched in a modern *Homo sapiens* than in any Neanderthal.

Clearly, preconceived notions of the inevitability of population mixing when the Cro-Magnons invaded the Neanderthal heartland are still deeply influencing interpretations of fossil morphology.

High-Tech Morphometry

Still, new techniques are beginning to influence old ideas. Thus, the penetration into paleoanthropology of the methods of "three-dimensional geometric morphometrics" (3DGM) during the late 1990s allowed a reassessment of the Neanderthals' position from a new perspective. 3DGM is a toolbox of quantitative approaches that allow more precise comparisons of form among objects than were permitted by more venerable multivariate statistical techniques. They do this by focusing on the coordinates of surface landmarks and on the geometric relationships among them. In paleoanthropology these new techniques have principally been applied to fossil skulls, and their most successful application to date has involved generating quantitative models of variation in skull form in other primate species and comparing them to the morphological distances observed between Neanderthals and modern humans. In 2004, New York University's Katerina Harvati and two colleagues compared the morphological distances between several model taxon pairs with observed distances between *Homo neanderthalensis* and *Homo sapiens*. The researchers found, unsurprisingly, that the choice of model pair greatly affected the outcome of the comparison. Yet they also found that Neanderthals showed an unusually high level of differentiation from modern humans—a degree of differentiation that strongly suggested independent species status for the two. Of course, different does not necessarily mean worse (or better, for that matter); and using equally sophisticated quantitative visualization techniques, California State University–San Bernardino's Wes Niewoehner and several colleagues demonstrated in 2003 that the unquestioned differences in finger anatomy between Neanderthals and moderns reflected no functional limitation on the part of the Neanderthals. Inferior dexterity thus could not have been a factor in their failure to develop tools matching the sophistication of those the Cro-Magnons brought with them into Europe.

A high degree of morphological distinction between *Homo sapiens* and *Homo neanderthalensis* implied a long period of independent evolution, and, entering the 1990s, the fossil record was not itself fine enough to allow paleoanthropologists to gauge the depth of this split very accurately. It had long been remarked that the German Steinheim cranium, discovered in 1933 but never the subject of a detailed monograph, exhibited certain features that linked it to the Neanderthals—though few went so far as to regard it as such. And at an estimated 225 kyr or so old, it was not much if any older than the earliest fossils actually regarded as Neanderthals. Going back in time, it took a lot of special pleading to describe the 500-kyr-old Mauer mandible, the type specimen of *Homo heidelbergensis*, as a linear precursor of the Neanderthals—though



Computer-generated model of a Neanderthal hand (based on La Ferrassie 1) showing stages in the apposition of the tips of the thumb and first finger. *Courtesy of Wes Niewoehner and NDSU Archaeology Technologies Lab.*

not all researchers found that an impediment. As we'll see in a moment, fossil material bearing on the question of Neanderthal antiquity—or at least of the antiquity of the lineage of which *Homo neanderthalensis* was the eventual outcome—had indeed been found by the time that the molecular systematists began to weigh in on this issue, but the dating of this material was uncertain, and it was the molecular people who first put an unequivocal (if not undebated) figure in years on the *neanderthalensis/sapiens* split.

Pääbo's student Matthias Krings and colleagues, in their 1997 paper reporting the very first Neanderthal DNA results, estimated that the human–Neanderthal ancestor lived about four times as long ago as the ancestor of all modern humans, which translated by their calculations to between 690 and 550 kyr ago. In 1999 they broadened this range somewhat to confidence limits of 741 and 317 kyr, with a 465 kyr central date. This range is wide enough to suit all observers, but the central date is beginning to look a little on the youngish side, especially in light of some very exciting fossil finds and datings made during the 1990s.

Atapuerca: A Fossil Cornucopia

The Atapuerca Massif is a very grand name for a smallish region of limestone exposed near Burgos, in northern Spain. In 1976 spelunkers exploring a solution cave known as the Cueva Mayor happened on a deep pit, now known as the Sima de los Huesos (“Pit of the Bones”)—a shaft descending vertically almost fifty feet into the ground and dead-ending in a small blind chamber at the base of a long talus slope. Exploring the pit they found the bones



Three-quarter view of Cranium 5 from the Sima de los Huesos, Atapuerca, Spain. *Photo by Ken Mowbray.*

of extinct cave bears, which they ultimately reported to the distinguished Spanish paleontologist Emiliano Aguirre. In 1984 Aguirre started excavations at the site, and following his retirement handed it over to a group of his students. Working in the stifling bottom chamber proved to be probably the nastiest job in paleoanthropology—but equally probably the most rewarding.

Well before 1991 hominid bones began to be found, but in that year undisturbed sediments were reached, and the hominids really began to roll in: since then, more than 5,000 hominid fragments have been recovered, adding up to the fractured remains of at least 28 individuals: infants, children, and adults of both sexes. How those numerous individuals came to be all jumbled up there at the bottom of the pit remains a mystery, although the excavators favor human (or at least hominid) agency—and the presence in the pit of only one artifact, a spectacularly beautiful rose quartz handaxe, suggests to them an element of ritual despite the broken-up nature of the bodies. Other researchers favor more prosaic explanations.

July 1992 was especially auspicious at the Sima, yielding over the course of the month an almost complete hominid braincase, parts of an immature skull, and “Skull 5,” which is finely preserved and remarkably complete, even though it had to be pieced together from dozens of fragments, many of

them very tiny. These were described in 1993 by Juan-Luis Arsuaga of the Universidad Complutense de Madrid and a team of colleagues. The cranial volumes reported for the two adult specimens were 1,390 ml for the braincase and 1,125 ml for the skull, and an estimated age was given of around 300 kyr on the basis of U-series dating of a flowstone by James Bischoff of the U.S. Geological Survey. Arsuaga and colleagues noted that in many but not all ways these crania were Neanderthal-like, a judgment that still stands today. Major later finds included a whole raft of bones of the postcranial skeleton, including a massive pelvis nicknamed "Elvis." This, too, had many Neanderthal-like features. A hefty summary of finds up to 1997 was presented in a special issue of the *Journal of Human Evolution*, in which Arsuaga and colleagues attributed the Sima specimens to the species *Homo heidelbergensis* and in which a detailed account of the geology of the site was given. Based on various U-series dates, a minimum age of 200 ka was proposed for the fossils, although the authors favored a date of over 320 ka. These dates have since been substantially revised backward; they crept back to 350 ka-plus in 2003 when a newly discovered and undisturbed capping flowstone was reported on, and in 2007 Bischoff and colleagues, using ultra-high-precision technology, redated the same flowstone to an astonishing minimum of 530 kyr—which placed the Sima hominids "at the very beginnings of the Neanderthal lineage."

But the Pit of the Bones is far from the only hominid site at Atapuerca. In the nineteenth century a British company dug a railroad cutting right through the Atapuerca Massif, inadvertently exposing several early hominid occupation sites in the process. Some of these have produced stone tools dating back as far as a million years, but the most exciting of them is Level TD-6 of the site known as the Gran Dolina, paleomagnetically dated to some 780 kyr ago, at the very end of the Early Pleistocene. This site is exposed vertically in the walls of the rail cutting, and the TD-6 level lies low down, making it hazardous to remove too much sediment before the overlying layers have been excavated away. However, in 1995 a test excavation produced several dozen hominid fragments belonging to at least six individuals, one of them an adolescent, parts of whose face were preserved. At the same time numerous artifacts were recovered, all of them rather unsophisticated, of Mode 1 type.

The preserved midface portion of the juvenile specimen, ATD6-69, was described in 1997 by Jose María Bermúdez de Castro of the Museo Nacional de Ciencias Naturales in Madrid and his colleagues as showing "a completely modern pattern of midface topography," although they found a constellation of more "primitive" characters in the teeth and brow area. All in all, Bermúdez de Castro and his colleagues found themselves unable to assign the Gran Dolina hominids to any existing taxon and proposed a new species for it: *Homo antecessor* ("pioneering man"). Indeed, they went beyond this and proposed that their *Homo antecessor* represented the common ancestor of the lineage that led to *Homo sapiens*, on the one hand, and to *Homo neanderthalensis* (via *Homo heidelbergensis*, to which they exclusively allocated

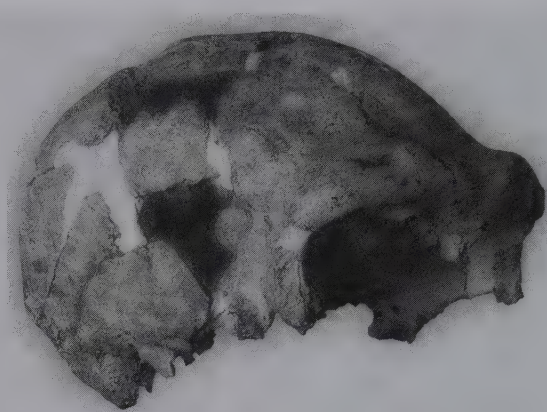


Associated facial fragments from the TD6 level of the Gran Dolina, Atapuerca, Spain. Holotype of *Homo antecessor*. Photo by Ken Mowbray.

all Middle Pleistocene European hominids—Sima, Steinheim, et al.), on the other. At that time they excluded *Homo erectus* from this picture entirely, but in 2005 they reported a more complete mandible from TD-6 in which they perceived particular resemblances to the Zhoukoudian mandibles from China. Accordingly they changed tack on the question of relationships and, while remarking on the closeness of *Homo antecessor* to the line leading to *Homo sapiens*, excluded the Gran Dolina species from the ancestry of the Neanderthals and others in their lineage. As this book goes to press the same investigators have reported an even older hominid jaw fragment, some 1.2 myr old, from yet another Atapuerca site, the Sima del Elefante; its affinities are still undecided.

Diversity Among Early Europeans

In early 1994, just before all the excitement started at the Gran Dolina, an Italian bulldozer operator building a road at a place called Ceprano, south of Rome, brought to light the fragments of a hominid skullcap. These were miraculously spotted by the archaeologist and paleontologist Italo Bidittu and were subsequently reassembled at various times by a team of Italian anatomists and paleontologists initially led by Antonio Ascenzi. The site itself,



The calvaria from Ceprano, Italy. Holotype of *Homo cepranensis*. Courtesy of Giorgio Manzi.

investigated by a team that included the veteran geologist Aldo Segre, was first thought to be about 700 kyr old, although later estimates lengthened to the 900–800 kyr range. The sequence of reconstructions eventually yielded a wide, relatively short, thick-boned braincase, fairly low and angled at the back, that had tall, somewhat twisting supraorbital surfaces and a brain volume estimated at up to 1,185 ml.

Whatever species this cranium represented, the juvenile from the Gran Dolina would not have grown up to resemble it at all closely, and in 2003 Francesco Mallegni and colleagues made it the type of the new species *Homo cepranensis*. Mallegni and his collaborators found that the “typical characters” of European *Homo heidelbergensis* were missing in the Ceprano specimen and compared it instead to a 1-myr-old cranium from Daka (a.k.a. Bouri) in Ethiopia, which had been described the year before. Brain volume in the Ethiopian specimen was said to be around 1,000 ml, and its describers had allocated it to *Homo erectus*. Mallegni and colleagues also found resemblances in Ceprano to the (probably much) later Kabwe skull from Zambia, which they regarded as belonging to its own species, *Homo rhodesiensis*. But while all of the Italian investigators seemed to agree, as the paleoanthropologist Giorgio Manzi put it, that both “Ceprano and the penecontemporaneous TD6 assemblage...show a closer link with the African trajectory toward *H. sapiens* than with the European fossil record of the Middle Pleistocene,” the Spanish contingent hewed much more to the view that the two hominids might actually in some way be versions of the same thing.

As early as 2001 the French paleoanthropologist Jean-Jacques Hublin published the notion that *Homo antecessor* from the Gran Dolina might actually belong to the same species as the 700-kyr-old jaws from Tighenif in Algeria that Camille Arambourg had named *Homo mauritanicus* back in the 1950s

(and should thus be known by the same name). When we reviewed the hominid fossil record for a volume eventually published in 2005, the University of Pittsburgh's Jeffrey Schwartz and I independently arrived at much the same conclusion. If all this is indeed the case, then both the Italian and the Spanish fossils have African counterparts, though almost certainly belonging to different lineages.

Pending more complete materials from TD-6 (which it's a very good bet will eventually be forthcoming), it is still difficult to know exactly where to place the Gran Dolina fossils in the human evolutionary story. In contrast, from the beginning there was no doubt that the Sima de los Huesos hominids were linked in some way to the Neanderthals. *Homo neanderthalensis* is an unusually easy hominid species to diagnose because of its many derived characters. In 1997 Arsuaga and his collaborators had assigned the Sima fossils to *Homo heidelbergensis* apparently because they were clearly not Neanderthals, even though they displayed many Neanderthal characteristics of the skull and pelvis. All well and good, then, that they were not *Homo neanderthalensis*, but this was hardly enough to make them *Homo heidelbergensis*. As you will recall, this latter species is based on Otto Schoetensack's Mauer mandible, a specimen that is peculiar in its very stout ramus, but that otherwise bears quite close resemblance to the most complete of the lower jaws from French site of Arago. And the Arago jaw, as we have seen, is matched by a fossil face that groups comfortably with such crania as those from Petralona, Bodo, Kabwe, and even Dali—but that does not look in the least like Skull 5 from the Sima. Schwartz and I noted this in a review published in 2003, in which we also pointed out that *Homo heidelbergensis* in the strict sense of Arago and its allies was contemporaneous with the Sima hominids, suggesting that more than one hominid lineage was present in the Middle Pleistocene hominid record of Europe.

Nonetheless, the spirit of the Synthesis lived on with gusto in the notion that all of the post-*Homo antecessor* hominid fossils from Europe must somehow have been part of an endemic lineage that culminated in *Homo neanderthalensis*. This belief was made very specific by the Atapuerca group, who clearly felt that any distinction made between the Sima hominids and *Homo neanderthalensis* would ultimately have to be an arbitrary one. And it fit very well with Hublin's "accretionary" notion of Neanderthal origins, most clearly articulated in 1998, which is probably the most widely accepted model of Neanderthal evolution today. According to Hublin, there was a progressive appearance of Neanderthal morphologies over time—initially in the face, then in the back of the skull, and finally in the skull vault. The first such features were detectable in "early pre-Neanderthals" such as Arago and Mauer—and possibly Ceprano, though Hublin excluded the Gran Dolina fossils; then came "pre-Neanderthals" like Steinheim and Swanscombe; after this followed the "early Neanderthals" such as Krapina and Saccopastore; and finally the "classic Neanderthals," exemplified by such specimens as La Chapelle-aux-Saints,

La Ferrassie, and Feldhofer. Interestingly, Hublin barely mentioned the Sima hominids in laying out this sequence, and the subsequent much earlier redating of this latter site certainly complicated the picture; but despite problems posed by actual morphologies the reductionist attractions of this schema, to a field still in many ways in thrall to the Synthesis, are evident enough.

Out of Africa for the First Time

There is certainly room for argument over potential links between such fossils as those from the Gran Dolina and Ceprano and later European hominids. Where there is a definite disconnect, however, is in the Caucasus, at Europe's farthest eastern reaches. For long it was believed that the first exodus of hominids from their natal continent of Africa had occurred at about a million years ago at most. So it came as quite a surprise when, in 1991, archaeologists excavating a ruined medieval town at Dmanisi, in the Republic of Georgia, discovered a hominid jaw among the remains of truly ancient animals poking out of the walls of storage pits that had been dug by the medieval townsfolk. Preliminary guesses that this fauna was 1.8 myr old have since been confirmed by dating of the underlying basalt, making this the oldest confidently dated hominid site known beyond the confines of Africa.

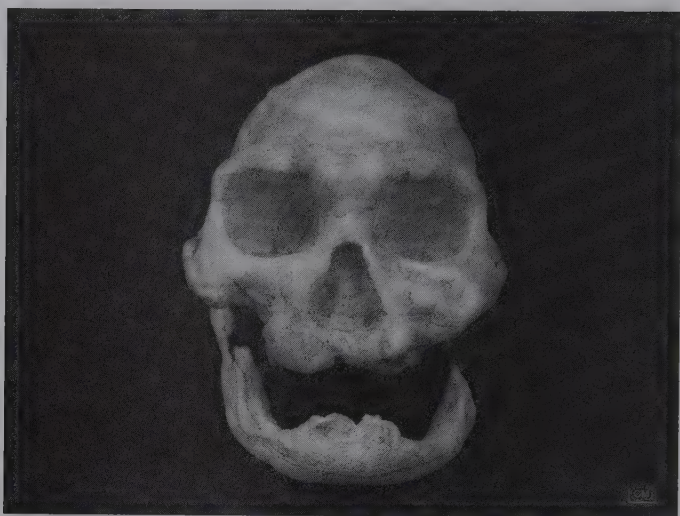
In 1995 the partial mandible was allocated by its describers Leonid Gabunia and Abesalom Vekua to "archaic African *Homo erectus*," a judgment with which most commentators were in general agreement. In 2000 Gabunia and colleagues reported the discovery at the same site of two more crania, which they considered comparable in size to their Koobi Fora *Homo ergaster* (a.k.a. *H. erectus*) counterparts, although they had very small cranial volumes of 780 and 650 ml. Stone tools found in association with these hominid remains were crude pebble tools of Mode 1 type. Soon, though, the picture became more complicated, with the discovery of a very large and long mandible with highly worn teeth. This jaw was very much bigger and longer than the one first found, but Gabunia and his coworkers nonetheless concluded that all of the Dmanisi hominids had belonged to a single distinctive and highly sexually dimorphic species that in 2002 they named *Homo georgicus*. Overall, the conclusion was that *Homo georgicus* "preserves several affinities with *Homo habilis* and *Homo rudolfensis*... foretelling the emergence of *Homo ergaster*."

Barely was the ink dry on this declaration than the group announced the discovery of an associated cranium and mandible that was strikingly different from those reported earlier. Although it was notably small-brained, with a cranial capacity of around only 600 ml, it was thought to resemble some of the Koobi Fora specimens of about the same age. Abandoning both the species *Homo georgicus* and the notion of *Homo ergaster* and *Homo erectus* as discrete entities, the team allocated the entire assemblage of Dmanisi hominids to *Homo erectus*, while noting that they "are among the most primitive individuals so far attributed" to that species.



Side view of the cranium and mandible D 2700/2735 from Dmanisi, Republic of Georgia. Photo of cast by Jennifer Steffey; 1-cm scale.

In 2002 and 2004, respectively, the cranium and mandible of another individual were recovered at Dmanisi. The most remarkable aspect of this presumed aged male was the fact that at death he had possessed only one single tooth and had apparently been almost entirely edentulous for many years. In 2005 David Lordkipanidze and colleagues surmised that, although at least one wild chimpanzee is recorded to have survived for many years without teeth, the Dmanisi individual must have “survived for a lengthy period without consuming foods that required heavy chewing...and/or by help from other individuals,” and suggested that this might have significant implications for early *Homo* social structure. In a review published shortly afterwards, the American paleoanthropologist Philip Rightmire and other Dmanisi team members reaffirmed their belief that the entire hominid collection from the site represented a single “paleodeme” that was best placed within *Homo erectus*, despite perceived resemblances to *Homo habilis* in brain volume and some aspects of facial morphology. If the large jaw indeed fit with the other specimens, they concluded, the correct nomen for the assemblage would be *Homo erectus georgicus*; if it didn’t, a new subspecies name would have to be found for the rest of the sample. Subspecies names are not, as I’ve noted, generally useful in paleontology; but finding two different subspecies of the same species at the same site would have far-reaching implications for the manner of its accumulation and would open the door to considering whether more than one species might not be involved. In 2005 Schwartz and I urged such reconsideration, and the reported discovery in 2006 of a cranium that articulates with the large mandible may well have a bearing on this issue, once it is described.



Front view of the edentulous cranium and mandible D 3444/3900 from Dmanisi, Republic of Georgia. *Photo of cast by Jennifer Steffey; 1-cm scale.*

The Dmanisi discoveries show that hominids exited Africa not long after the earliest date at which we can reasonably suppose that members of the genus *Homo* had acquired modern body size and proportions. Yet the stone tools found at Dmanisi are crude, and the hominids' brains were small. What, then, might explain the newfound ability of hominids to disperse away from their home continent after some 4–5 myr of confinement? If it wasn't greater intelligence, which restricted brain size suggests it was not, and if it wasn't better technology, as the tools suggest it was not, the only obvious alternative was modern striding locomotion.

That this may indeed have been the key was strongly reinforced when, in 2007, David Lordkipanidze and colleagues reported on postcranial bones recovered from Dmanisi, including parts of a skeleton associated with the third cranium. These authors reported that the Dmanisi postcranials showed a combination of primitive and derived features. However, the principal primitive character these authors pointed to was small body size (stature well under five feet), while the lower limbs, especially, showed a constellation of derived features in common with later *Homo*. All in all, the conclusion was that the Dmanisi hominids, despite their short stature, had possessed "modern-human-like body proportions and lower limb morphology indicative of the capability for long-distance travel."

Moving East

Where else might we look for evidence relevant to this matter? Pickings are slim. A number of other sites on the Asian landmass have been reported to



Lateral view of the SM3 braincase from Sambungmachan (Poloyo), Java. *Photo courtesy of Sam Marquez.*

harbor evidence of early human presence, among them a site in Pakistan called Riwat, whence crude 1.6-myr-old stone tools, but no hominid fossils, were reported in 1989. Some time later a possible 1.9 myr date was given for a reportedly hominid lower jaw fragment, a couple of incisor teeth, and some crude tools that were found in 1996 at Longgupo Cave in southern China. However, both fossils and tools are in dispute, not to mention the date, and all must remain in a suspense account for the time being. In 1994 the geochronologist Carl Swisher and colleagues reported a $^{40}\text{Ar}/^{39}\text{Ar}$ date of 1.8 myr for volcanics associated with the presumed *Homo erectus* from Mojokerto in Java. Largely because of questions about the specimen's exact provenance, that date has also been disputed—though the ancientness of the specimen doesn't appear to be in question—and in any event there are no archaeological or postcranial associations. Furthermore, the specimen was that of an infant.

In 2004 the French paleoanthropologist Hélène Coqueugniot and colleagues capitalized on this last fact. They analyzed the specimen and estimated the individual's age of death as about one year. At this tender age the infant had a cranial volume of between 72 and 84 percent of adult *Homo erectus* size; this implied a pattern of relative brain growth resembling that of apes, but strongly distinct from that of modern humans. The inference from this was that the individual—and by extension *Homo erectus* in general—had differed significantly from us in its pattern of cognitive development. What this means for the role of cognition in facilitating hominid movement out of Africa is a matter for conjecture. But it certainly does not conflict with inferences from Dmanisi; and the penecontemporaneity of Dmanisi and Mojokerto is supported by the fact that Swisher and colleagues derived a

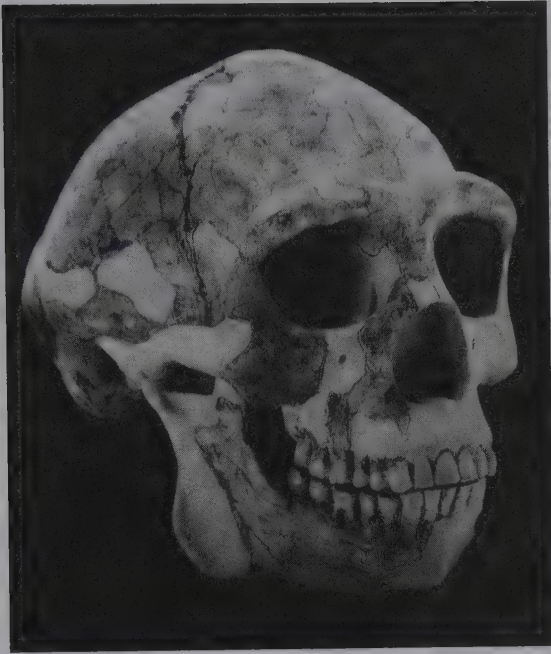
1.66 myr date for a site at Sangiran that had yielded a couple of crushed "Meganthropus" crania.

During the 1990s and the early years of this century, new Javanese hominid fossils continued to turn up as a result both of deliberate fieldwork and of serendipitous discoveries by farmers. Indeed, one partial cranium surfaced in a natural history store in New York City in 1999; after study at the American Museum of Natural History it was returned to Indonesian custody by the store's owner. The specimen became known as Sambungmacan 3 (SM3) because it is believed to have come from close to a site of that name in central Java that had yielded a rather similar-looking calvaria (SM1) in 1973. SM2 was a tibial fragment also found nearby, and a third cranium (SM4), with a well-preserved cranial base, was found later and described in 2003 by a Japanese group. Quite similar in appearance is a calvaria, briefly published in 1990, from a place called Ngawi that lies a little to the east of Sambungmacan. None of these specimens has good provenance information, or any archaeological context, but all are guessed to be fairly young, geologically speaking: an age of 200 kyr or less is probably reasonable for all.

Throughout this period new specimens also continued to appear periodically in the classic Javan collecting region of the Sangiran Dome. However, one of the biggest surprises came not from a new fossil, but from the redating of an important if rather neglected series of prewar fossils. The extensive series of crania from Ngandong had long been suspected to be on the youngish side geologically, but a redating in 1996 by Carl Swisher and colleagues, using ESR and U-series on bovid teeth from the hominid-bearing levels at the locality, yielded an altogether unexpected range of between 27 and 53 kyr. This suggested not only an extraordinarily long duration for *Homo erectus* on Java, but also the survival of this species into the period when modern humans first colonized southeastern Asia.

After more than a century of constant accretions, *Homo erectus* had come to be the default hominid of a vast stretch of the Pleistocene, and the species embraced a very large proportion of all specimens belonging to fossil *Homo*. Still, partly because it was very difficult to divide this mass of fossils up into discrete and easily definable units, most paleoanthropologists were nonetheless content to sweep this vast variety of differing morphologies into a single species *Homo erectus* that varied greatly in space and changed substantially over time (notably in brain size). In addition, this situation was just what the Synthesis had predicted, and was hence in tune with many paleoanthropologists' theoretical expectations. But by normal mammalian standards this much variety in any species was worrying, and in the late 1990s Jeffrey Schwartz and I began to feel it was time to reexamine the evidence.

In any taxonomic analysis, especially one that involves allocation of fossil specimens to species, it is necessary to start with the holotype and work outward from there. If you do this, you derive a very different perspective than the one you get from taking an existing accretionary intellectual construct and



Three-quarter view of the 1996 Sawyer/Tattersall reconstruction of the skull of Peking Man, using casts of "Skull IX" and various facial and mandibular fragments from Zhoukoudian Locality 1. Unlike its largely imaginative predecessor, this reconstruction possesses original bony continuity from top to bottom and from side to side. *Photo by Jennifer Steffey; 1-cm scale.*

trying to fit new fossils into a few predetermined categories (that are anyway arbitrary, even in principle). In the case of *Homo erectus*, the type specimen is Dubois's Trinil skullcap from Java. Defining the species as it does, this is the only specimen in the entire hominid fossil record that we *know* for certain is *Homo erectus*.

The Trinil 2 skullcap is highly derived among hominids in several features, particularly of the brow and the rear of the skull. Although the hominid sample from the adjacent Sangiran region is quite variable, especially in robusticity, the basic morphology of the Trinil braincase is repeated in most comparable Sangiran specimens, which are also of generally comparable age. The only major exception to this is, indeed, the Sangiran 17 cranium, but it is an arguable exception. Moving outward a bit farther, the Sumbungmacan/Ngawi specimens are both younger and different in a variety of characteristics, including a contrasting brow structure. The braincases appear better "inflated" than in the Trinil form, and taken together these fossils form a "morph" that generally resembles the Trinil type but is nonetheless distinguishable from it. If we then look at the Ngandong specimens, we also find

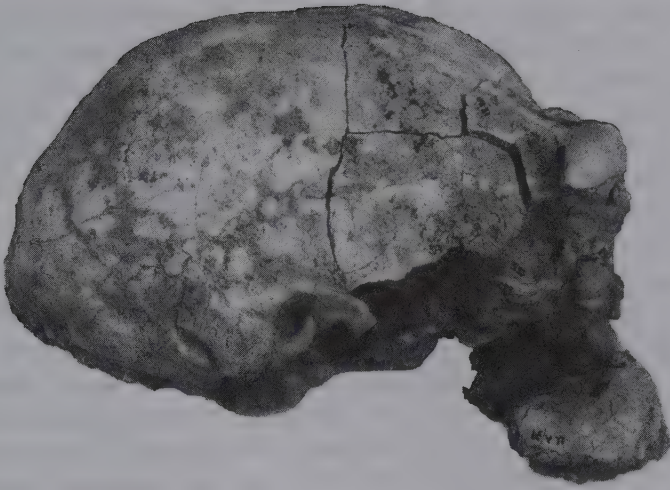
them to be distinctive. They differ from the Trinil/Sangiran form in the same way that the Sambungmacan group does, but they are larger and more robust than the latter, showing higher endocranial volumes and vertical-sided braincases with stronger rearward projection. In short, together all these Javan fossils present a uniform overall morphology, especially of the supraorbital and occipital regions, within which distinctive groupings may be observed.

Whether or not you wish to divide up this Javan group is essentially a matter of taste; there is no “silver bullet” that will allow us to determine whether we have one species in the assemblage or three. When we published this view, first in 2000 and later in our overall review of the hominid fossil record in 2005, Schwartz and I would have been happy to have only one species—incredibly long as was the time spanned by *Homo erectus* thus viewed. But whatever one’s exact opinion on this matter, clearly here was the “core” group by which the identity of *Homo erectus* had to be judged. And a similar pattern applied when we broadened the comparison to include other eastern Asian forms traditionally allocated to *Homo erectus* such as those from Zhoukoudian. In eastern Asia there was definitely an endemic *Homo erectus* clade—an indigenous hominid radiation—whether or not you might want to divide it up into multiple species.

“African *Homo erectus*”: More Diversity?

But when we broadened the comparisons yet further, to Africa, the picture changed. Indeed, the range of fossils that had at one time or another been allocated to *Homo erectus* appeared as an unusually motley assortment. This had first been recognized as far back as 1975, when Colin Groves and Vratja Mazak had created the new species *Homo ergaster* for the lower jaw ER 992—but the reality, as it turned out, was yet more complex than this. The iconic ER 3733 cranium actually differs quite radically from the slightly younger ER 3883 cranium, and both in turn differ quite strongly from the Turkana Boy cranium, WT 15000—the lower dentition of which contrasts with that of ER 992. We are looking here at a heterogeneous assemblage that has none of the unifying *Gestalt* of the Java clade. And, indeed, this might not be unexpected. Africa in the period between about 2 and 1.5 myr ago seems to have been a hotbed of evolutionary experimentation, paving the way for later developments in human evolution, while the *Homo erectus* group was to continue treading evolutionary water in its isolated enclave over a vast period of time—until, quite possibly, it met its end at the hands of newly arriving *Homo sapiens*, just as may have been simultaneously happening to *Homo neanderthalensis* at the opposite end of the Eurasian continent.

This way of looking at things did not, however, catch on. New finds from the Middle Pleistocene in East Africa, for example, continued routinely to be assigned to *Homo erectus*, no matter what they looked like. Thus in 2004 a group led by the Smithsonian’s Rick Potts, one of the most thoughtful of



Lateral view of the the Buia cranium from Eritrea. *Courtesy of Roberto Macchiarelli.*

paleoanthropologists, assigned a partial Acheulean cranium from Kenya's Olorgesailie to *Homo erectus*. Just under a million years old, and thus in the time range of Sangiran *Homo erectus*, this lightly built specimen does not resemble the type material from Trinil in the slightest: it is tiny, with slight projecting thickenings arching delicately over each orbit, in stark contrast to Trinil's shelflike and laterally flaring supraorbital surfaces.

Still, some flickers of recognition of complexity in the hominid fossil record seem to be emerging. Perhaps most indicative of a conflicted mindset was the publication in 2007 by Fred Spoor and colleagues of a couple of new fossils from Ileret in East Turkana, both dated not far off 1.5 myr. One of them was a maxilla with very worn teeth, ER 42703, which they allocated to *Homo habilis*—a species that, as we have seen, is every bit as much of a taxonomic basket case as *Homo erectus*. The other was a very small cranium, ER 42700, which they attributed to the latter. Spoor and his collaborators cited a few trivial “Asian characters” in defense of this assignment, but in fact this specimen shared none of the major diagnostic characters that make the Trinil holotype so distinctive. The only way in which this specimen might have made sense as a *Homo erectus* was under the ecumenical view that saw this species as an Old World-wide “stage” in a unilinear process of human evolution; yet the major conclusion that Spoor and colleagues drew from the new evidence was that multiple lineages of *Homo* were present in the Turkana basin 1.5 myr ago! In other words, the message in 2007 seemed to be that, while paleoanthropologists were beginning to recognize that the multiplicity of fossil hominid morphologies over the Lower Pleistocene required recognition and

analysis in terms of systematic diversity, they still remained too attached to traditional unilinear concepts of human evolutionary “stages” or “grades” to abandon them.

In 1998 a group of Italian and Eritrean researchers announced the finding of a distorted but fairly intact cranium, with a braincase volume of 995 ml, in 1-myr-old deposits at a site called Buia, in Eritrea’s Danakil Depression. Some postcranial fragments, believed to be of the same female individual, were also found at the same time. In their initial report the researchers found that the cranium had a “mixture of characters typical of *H. erectus* and *H. sapiens*,” a judgment that remained unchanged in 2004 after the “erectus-like” specimen had been cleaned and restored. Interestingly, as far as can be told from published illustrations of the latter, the appearance of this cranium differs quite strongly from that of the penecontemporaneous cranium from Daka, in neighboring Ethiopia. On its description in 2002 by an Ethiopian–American team led by T. D. White, this latter specimen was unequivocally assigned to *Homo erectus* and was said to show that “the early African and Eurasian fossil hominids represent demes of a widespread paleospecies.” What’s more, “its temporal and geographic position indicates that African *Homo erectus* was the ancestor of *Homo sapiens*.” A bold assertion indeed, especially in view of the very derived cranial structure of *Homo sapiens*, which is actually rather poorly foreshadowed in the fossil record.

Early *Homo sapiens*?

The same Ethiopian–American group was on firmer ground, however, when in 2003 it described some Pleistocene remains, principally an adult and an immature cranium, as early anatomically modern *Homo sapiens*. Although only pictures and a very sketchy initial description are available, and the authors found that the adult specimen lay “morphologically just beyond the range of variation seen in [anatomically modern *Homo sapiens*],” this seems a reasonable preliminary identification. The specimens came from a place called Herto in Ethiopia’s Middle Awash region; and what was most remarkable about them was firm dating to 160–154 kyr ago and their association with both Acheulean and Middle Stone Age stone tools. Although the very early date was consistent with expectations from molecular studies, it was a great deal earlier than any other reliable date then available for a modern skull; and doubtless because of that great age, the describers allocated the specimens to a new subspecies, *Homo sapiens idaltu*. And they went further, suggesting a direct evolutionary sequence that ran: *Homo rhodesiensis* → *Homo sapiens idaltu* → *Homo sapiens sapiens*. That’s as may be; but the early dating was soon made to seem entirely humdrum. In 2005 the geochronologist Ian McDougall and colleagues published a new date for the southern Ethiopian Omo Kibish crania, discovered decades before by Richard Leakey. As you will recall, one of these specimens looked rather modern, and they were both thought to be old; but everyone

was blown away by the new date (achieved by some fancy long-distance correlation, but expressed with confidence by its authors) of 195 kyr.

The first and more modern-looking of the two Kibish crania had been reconstructed to look pretty much like a modern *Homo sapiens*, but it lacked two of the most striking of the cranial specializations shared by modern human beings. These are the “bipartite” brow ridges, whereby the bony eminences above the eyes (usually but not invariably small) are divided by oblique grooves into central and lateral portions, and, in the lower jaw, the chin. As Schwartz and I pointed out in 2000, in modern humans this is not simply a bony swelling at the bottom of the jaw, but is instead a complex structure in the form of an inverted T. Besides Kibish 1 (and maybe Herto, too; it’s hard to tell), a few other African skulls, most of them unfortunately poorly dated but some of them quite recent, also lack these distinctive features while being indistinguishable from moderns in other respects.

Whether this means that these fossils are not *Homo sapiens* but simply very close relatives, or that the features concerned are *Homo sapiens* characteristics that are simply occasionally lacking, is anybody’s guess at the moment. But if you lump the two kinds together—regular moderns and the nonbipartite individuals without the complex chins—you have a grouping that does not very closely resemble anything else in the fossil record. Nothing is known, for example, that approaches this group as closely in diagnostic characters as the Sima de los Huesos individuals resemble Neanderthals. All of the “archaic *Homo sapiens*” specimens have their own peculiarities that distance them in one way or another. Perhaps this is the price you have to pay for doing systematics in a cluster as closely knit as the members of the genus *Homo*. But it does on the face of it suggest that *Homo sapiens*, certainly in the inclusive sense, originated in a major developmental reorganization of systems throughout the body, as a result of what was probably a relatively simple modification in DNA terms.

Evo-Devo

That it is possible nowadays to make a statement like this so confidently, without sounding like a nineteenth-century saltationist, is due to a major advance in our perspective on evolutionary processes that came about during the waning years of the twentieth century. This was the emergence of what is known as “evo-devo” (evolutionary developmental biology): a wide-ranging field that studies the constraints that developmental processes place on evolutionary change, and how changes in those processes promote it. One of the major aspects of evo-devo is the recognition of modularity in animal organization and of how integrated structural complexes may be radically modified by relatively simple changes at the level of gene structure. The rapid recent development of the fields of proteomics (how proteins function) and transcriptomics (how genetic instructions are transcribed), out of the not much

older molecular genetics and genomics, has shown that gene expression is just as important in evolution as gene structure, and it has emphasized just how complex the relationship is among changes at the genetic, developmental, and evolutionary levels. Since the 1950s the “central dogma of molecular biology” had been that genes were particular strips of DNA, and that the information contained in the DNA flowed just one way: DNA \rightarrow RNA \rightarrow protein. Now we are beginning to realize that things are in fact much more complex than this. It turns out that multiple overlapping genes can cohabit on the same stretch of DNA, and may produce RNAs that do not code for proteins but instead play significant roles in gene regulation.

This burgeoning recognition of the complexity of genomic processes has the potential to yield considerable insights into the nature of evolutionary change. For example, the traditional expectation was that modern human body proportions should have emerged gradually under the beneficent hand of natural selection from the more “archaic” proportions exhibited by the early “bipedal apes.” This was why, for instance, the apparently sudden advent of radically different modern form in the Turkana Boy came as such a surprise. But once this unexpected finding is placed in the context of gene regulation and expression, it is much easier to understand at least in principle what actually happened. For now we know that relatively small changes in the structure of genes can have cascading consequences throughout an individual’s growth and form.

Such a change, minor at the structural genetic level, may well have been involved in the origin of *Homo sapiens* as the anatomical entity we know today. Harvard’s Dan Lieberman and his colleagues, for example, pointed out in 2001 that a whole slew of developmentally coordinated changes, primary among them the retraction of the face, lies at the root of the structural uniqueness of the human skull. What is more, the contrast between a modern human skeleton and the Neanderthal reconstructed at around the same time by Sawyer and Maley showed how widely other changes, presumably resulting from the same genetic event, are distributed around the body skeleton. Still, if the evidence from Herto is to be taken at its face value, cognitive innovation in *Homo sapiens* did not superimpose directly on to this physical innovation, which we may reasonably estimate took place at some time in the period between about 200 and 150 kyr. No *significant* behavioral change is detected in the archaeological record until well after *Homo sapiens* had been established as an anatomical entity. The Herto fossils, for example, are associated with Middle Stone Age and even Acheulean stone tools; 70 kyr later, anatomical moderns at Jebel Qafzeh were apparently using a stone tool kit effectively identical to the one wielded both earlier and later by undoubted Neanderthals.

A “Human Revolution”?

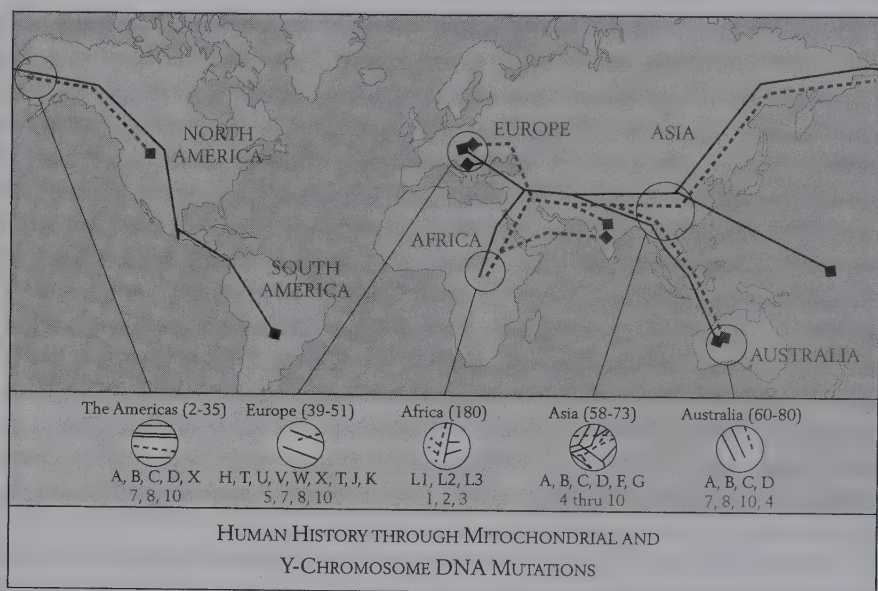
This is not to say that nothing behavioral of interest was happening in the Middle Stone Age of Africa. In a well-documented and carefully argued paper published

in 2000, the archaeologists Sally McBrearty and Alison Brooks attacked the notion of a “human revolution” in which modern behaviors had emerged suddenly and late. They pointed out that in Africa there was evidence for such sophisticated behaviors as blade making, pigment processing, and the use of grindstones over 200 kyr ago; that shellfishing and long-distance exchange of objects were taking place well over a hundred thousand years ago; and that such activities as flint mining and fishing went back almost to that point. Instead of a “revolution,” they saw an accretionary pattern of complex behaviors over the past quarter- or half-million years or so. Significantly, though, virtually all of the behaviors to which McBrearty and Brooks pointed were economic in nature, and it is arguable whether we can read the presence of the modern symbolic cognitive style into any strictly economic Old Stone Age behaviors. This is not to say that hominids of the period in question (including *Homo sapiens*) were unintelligent, or even that their behavioral repertoires were not becoming more complex; it is simply to say that they did not show the *kind* of intelligence that the Cro-Magnons, for example, displayed in Europe.

None of this means that the Cro-Magnons were the first-ever hominids to exercise symbolic intellectual capacities. Indeed, the first stirrings of the modern symbolic sensibility are found not in Europe but in Africa. But these signs come relatively late, although their antiquity has been pushed back substantially in the last decade. In 2002 the archaeologist Christopher Henshilwood and a group of colleagues reported the discovery at Blombos Cave, a coastal site near the southern tip of Africa, of several pieces of ochre that were apparently intentionally engraved, one with a quite complex geometric pattern. Not everyone agrees; but these pieces, found in an archaeological layer containing burned flints thermoluminescence dated to some 77 kyr ago, are by now widely accepted as the earliest evidence of symbolic behaviors yet found. In 2004 the same team reported finding perforated invertebrate shells in a 75-kyr-old layer at the same site. They believed that these shells were deliberately perforated for stringing as beads, and personal ornamentation is among the most symbolic of human activities. Significantly, the stone tools associated with this evidence for symbolism remained steadfastly Middle Stone Age, reinforcing the disconnect between economic and symbolic activities. This is also true for reportedly pierced shells from layers over 100 kyr old at Skhūl in the Levant.

“Adams” and “Eves”

Interestingly, soon after this period of occupation of Blombos Cave, South Africa underwent a period of aridification that seems to have largely emptied it of human occupation for several tens of thousands of years. Whether those stirrings of symbolism (as indeed, those at Skhūl) were the lineal antecedents of later such manifestations elsewhere might therefore be somewhat in doubt. What is clear, however, is that the modern human form originated in Africa and that the modern human sensibility emerged significantly later, albeit



Map showing the spread of *Homo sapiens* out of Africa and throughout the world, based on mtDNA and Y chromosome data. After Rob DeSalle and Ian Tattersall: *Human Origins: What Bones and Genomes Tell us About Ourselves*, 2007.

probably in the same continent. But for the details of the spread of anatomically and behaviorally modern humans beyond Africa, for want of fossils—or of ways of extracting the necessary information from the ones we have—we have to turn to the molecular record. We have seen that mitochondrial DNA, transmitted through the female line, provided the first molecular indication of the place of origin of *Homo sapiens*, and it was soon joined by the study of its male equivalent, Y chromosome DNA (only males have Y chromosomes). It turns out that these two lines of evidence (“Eves” and “Adams”) yield somewhat different histories; but this is not surprising when we consider the relative mobilities of the two sexes in historically documented societies.

During the 1990s various groups, including one led by Henry Harpending of the University of Utah, reported finding molecular evidence for a severe bottleneck in the human population about 80 kyr ago. It is assumed that it was the “expansion wave” that followed this drastic reduction in the human population, that propelled the ancestors of all modern human beings outward from a central point of origin, probably in East Africa, and then beyond the continent. To summarize a large number of studies, three “Eve” lineages remained confined to Africa, while about 60 kyr ago six “Eve” lineages emigrated to Asia, and 20 kyr after that nine migrated to Europe. Three “Adam” lineages stayed in Africa, and about 60 kyr ago seven “Adam” lineages moved into Asia, all of them moving into Europe around 40 kyr ago.

Looked at in finer grain, the same molecular markers can be used to trace local population movements within these vast areas; but of course, this is not strictly the "Fossil Trail." There is one unexpected fossil coda, though. Just like names, individual lineages passed through just one sex can go extinct, and will do so randomly. In Australia, mtDNA has been extracted from an ancient specimen, the lightly built Mungo 3 individual, which is around 40 kyr old. The overall DNA signature of Mungo 3's mtDNA is clearly *Homo sapiens*, but it is not found anywhere else, either in living or in fossil human beings (including nine other ancient Australians also studied). The ancient Mungo 3 thus seems to be our only known witness to an early-diverging mtDNA lineage that has subsequently been entirely lost.

The Mysterious Hominid of Flores

Perhaps the most extraordinary and unexpected paleoanthropological discovery since the original Neanderthal find was announced in late 2004, when an Australian–Indonesian group announced the finding, on the island of Flores to the east of Java, of a partial skeleton and some other bits of a new hominid they called *Homo floresiensis*. The skeleton came as a total surprise to everyone, consisting as it did of the bones of a tiny-brained (400 ml) adult individual who had stood barely over three feet tall—and had died only some 18 kyr ago! Other hominid teeth and bones scattered through the deposits at the site of discovery, Liang Bua cave, were eventually bracketed by radiocarbon and TL dates to the period between about 95 and 14 kyr.

The skull of the first individual, LB1, was like nothing anyone had ever seen. The longish and low braincase was small, but so was the rather flat face that lay beneath delicate brow ridges which arced separately above each eye. The mandible lacked a chin, and the teeth in it were small. When describing this strange phenomenon as belonging to a new species of the genus *Homo*, Peter Brown of Australia's University of New England and a group of colleagues expressed the view that the Flores hominid was a probable survivor of a *Homo erectus* population that had somehow become isolated on the island of Flores, which (unlike Java) had never been connected to the Asian mainland.

The small stature of *Homo floresiensis* was attributed to the dwarfing effect that is not at all uncommon among island populations of vertebrates; indeed, the Liang Bua deposits also yielded a dwarfed version of the extinct proboscidean (elephant) genus *Stegodon*. In 2005 Michael Morwood and the rest of the Liang Bua team reported further finds from the cave. These included more of the original skeleton and a second adult mandible which confirmed that the rather unusual morphology of the first had been no freak. There were also archaeological associations, including the reported use of fire at Liang Bua. Previous archaeological prospections had turned up simple stone tools at another site on Flores that dated to over 800 kyr ago. But some of the stone tools found



Three-quarter view of the LB1 hominid skull from Liang Bua, Flores, Indonesia. Restoration by G. J. Sawyer, based on a stereolithograph. Photo by Jennifer Steffey; 1-cm scale.

at Liang Bua were much more sophisticated than these, and included not only blades and perforators but microblades that must have been hafted.

Immediately dubbed “the Hobbit” by the press, the new find sparked an instant furor. One of the first critics was the Field Museum’s Bob Martin, an expert on the relationship between brain sizes and body weights in mammals. The Liang Bua crew had reasonably estimated a body weight for LB1 of around 50–80 pounds, but in 2006 Martin and a group of colleagues calculated, on the basis of several different scaling models, that if you shrank the brain of *Homo erectus* to Flores size you would end up with a totally impossible body weight of about 25 pounds. Martin and coworkers concluded that the tiny size of the Hobbit’s brain could not have been achieved by any normal process of species dwarfing. Instead, it must have been due to a pathology, suggesting that LB1 was a microcephalic modern human.

This possibility had actually been dismissed the year before by the paleoneurologist Dean Falk and colleagues, who had found that the brain of LB1 had generally resembled that of *Homo erectus* in shape, even though its brain/body ratio scaled like an australopith. The researchers were impressed by the complex convolutions (especially of the frontal lobes) that they saw on the endocast of the brain. These suggested to them that there had been some elaboration of higher function, and although they felt it unlikely that this could be the brain of a scaled-down *Homo erectus*, they thought it possible that the Flores hominid might have shared a small-brained ancient ancestor with *Homo erectus*. Either way, though, this was not just a pathological

version of something else—a conclusion that was supported the same year by an Australian group led by Debbie Argue.

Still, the pathological explanation soon found itself back at center stage, now promulgated by a group led by the veteran Indonesian paleoanthropologist Teuku Jacob, who contended that signs of abnormal growth and development were present in both the skull and the postcranial bones of LBI. The conclusion here was that the Hobbit was a pathological member of a very small-statured *Homo sapiens* population that had been endemic to Flores. Around the same time, Gary Richards of the University of California at Berkeley published the notion that the Flores morphology was that of a modern human afflicted with a growth hormone deficiency, combined with a mutation in a specific gene family that was involved in producing some of the human syndromes involved in what is broadly known as microcephaly. Accordingly, Richards found no reason to regard LBI as anything but an abnormal modern human, though possibly not an abnormal member of the particular population he or she represented. A similar theme was struck in 2007 by a team of Israeli anatomists, who thought LBI was a good candidate for Laron syndrome, a congenital deficiency of growth hormones. This condition often shows multiple occurrences in families and small isolated populations, and thus might have been responsible for an abnormal local human population in Flores.

Still, at a meeting in 2006, Bill Jungers and Susan Larson of Stony Brook University presented convincing reasons for believing that the Liang Bua bones did not show typical signs of pathology and that the unusual morphology of the specimens was “real,” representing the normal anatomy of a very unusual hominid population with very deep roots and some highly unique specializations of the postcranial skeleton as well as of the skull. And in 2007 Matthew Tocheri and colleagues reported that the wrist bones of LBI were nothing like those of modern humans, lacking a set of distinctive features that are found in *Homo neanderthalensis* as well as in *Homo sapiens*. Instead, the researchers found resemblances to very ancient hominids, including “Lucy” and *Homo habilis*. The morphology concerned is also found in apes, and the conclusion was that LBI’s wrist anatomy is that of a very primitive hominid (in this respect), not of an abnormal modern human. The debate continues.

Even this brief survey of opinion on the Flores question is enough to show that, by a country mile, this is the most hotly argued issue in paleoanthropology yet to surface in the twenty-first century. Perhaps this is ironic (or, more to the point, instructive), for whatever Flores is (and chances are that it is a “real” entity that will have to be explained in evolutionary rather than pathological terms), it is a strictly local phenomenon. However the argument is eventually resolved, it will have little bearing on the larger picture of human evolution as it played out toward the end of the Pleistocene. Nonetheless, it may well provide yet another example of a hominid species that, after a long independent evolutionary history, found itself in the end unable to cope with the appearance on the scene of the new and unprecedented phenomenon of *Homo sapiens*.

CHAPTER 18

Back to the Beginning

For almost two decades *Australopithecus afarensis* held the “oldest hominid” title. But its reign came to an end abruptly in 1994, when a new contender entered the fray, championed by Tim White, one of the original namers of *A. afarensis*. With two colleagues, White described a handful of distinctive fossil fragments from the site of Aramis, in Ethiopia’s Middle Awash region, as members of the new species *Australopithecus ramidus*. Dated to about 4.4 myr ago, the *A. ramidus* materials were a good half-million years earlier than anything that had been called *A. afarensis*, and they included some pieces of jaw with teeth, some postcranial fragments, and, most significantly, part of the base of one individual’s skull.

A Veritable Menu of Earliest Hominids

The search for the earliest hominid had always been something of an ad hoc affair, governed as much by considerations of time—and even sometimes by wishful thinking—as of actual morphology. And the description of *A. ramidus* as an ancient human ancestor had much of that traditional flavor. If this new form were actually a hominid, then it certainly well predated any other hominids then known; and if it really was old, then it had to be “primitive.”

This mindset permeated the description of *A. ramidus*. “Canine reduction” had long been one of the morphological touchstones of being hominid, and the describers noted that although the canine teeth of *A. ramidus* were larger than typical of *Australopithecus* species relative to the teeth behind them, they were smaller than in any ape and were more “incisiform,” with the front and back surfaces meeting at a blunter angle when seen in profile. This observation accorded with the prevailing belief that a “honing complex” (involving the lower canine and first premolar, and the primitively large upper canine that occluded between them) had been progressively lost in the “ape-hominid transition.”

Yet in contrast to that of any incisor, the profile of the upper canine of *A. ramidus* was both pointed and broadly reminiscent of that of a female

orangutan; even more puzzling for a supposed hominid was the fact that the surprisingly narrow premolar and molar teeth of the Ethiopian fossil showed only thin coatings of enamel—and thick enamel was widely taken as one of the most characteristic features of early hominid teeth. What most caught people's attention, however, was the fragment of skull base. In the authors' own words, "the major anatomical/behavioural threshold between known great apes and Hominidae is widely recognized to be bipedality and its anatomical correlates," and in the cranial base fragment they found evidence of a forwardly placed foramen magnum—one of the inferred features that had tipped Raymond Dart off to the hominid status of *Australopithecus africanus* back in 1925. Interestingly, the associated fauna indicated that *A. ramidus* had probably lived in a fairly closed habitat; but the presumption of bipedality was enough to confer a hominid identity—whether or not it was likely that more than one hominoid lineage might have adopted terrestrial bipedalism as a solution to the late Miocene shrinking of the ancestral arboreal habitat.

In their original description, White and colleagues noted that *Australopithecus ramidus* departed from *A. afarensis* in several "key traits" shared by that species with later hominids. Perhaps it was not surprising, then, that in 1995 they changed their minds and placed their new species in its own genus, *Ardipithecus*. Oddly, they did this not in the form of a reevaluation of the evidence, but as a correction to their original paper—although in 1994 they had, perhaps, already foreshadowed this move by remarking that "the anticipated recovery at Aramis of additional postcranial remains... may result in the reassessment of these remains at genus and family level." Those postcranial remains were reportedly recovered shortly thereafter, and the fact that they remain unpublished well over a decade later may imply that a family-level reassessment, of the kind to which White and colleagues referred, cannot be ruled out.

Perhaps not, though; for soon the Middle Awash group added new material that extended the concept of *Ardipithecus* as the first hominid. In 2001 the team member Yohannes Haile-Selassie reported new specimens from a number of Middle Awash localities, all apparently laid down in wooded environments, which dated from between 5.8 and 5.2 myr ago. Mostly teeth or bits of jaw, but including a few postcranial fragments and an intact toe bone, these pieces were all assembled under the name of *Ardipithecus ramidus kadabba*, a subspecies that was three years later raised to species level as *Ardipithecus kadabba* on the basis of a few more teeth. The entire collection was a bit miscellaneous, but the teeth appear to be thin-enamelled like those from Aramis, and the canines are yet more pointy, though Haile-Selassie described them as "early manifestations" of the incisiform pattern. The bulk of the *Ar. kadabba* fragments came from the 5.8- to 5.6-myr time zone; the foot bone was found several kilometers away from the others, and at around 5.2 myr was younger, raising the question of whether sufficient grounds truly existed for placing it in the same species. The toe bone itself is somewhat curved;

Haile-Selassie found its morphology quite similar to what is seen in the toe bones of *A. afarensis*. To him, then, it presented *prima facie* evidence of terrestrial bipedality. Not everyone saw it this way, though, and soon the French researcher Brigitte Senut declared that the curvature might equally argue for arboreal adaptation.

Millennium Man

This reaction on Senut's part was perhaps unsurprising, for in his initial description of *Ar. kadabba* Haile-Selassie had been rather dismissive of a new contender for "earliest hominid" status that had just been announced by Senut and colleagues. This "Millennium Man," bits of which were recovered in 2000 from four sites in the Tugen Hills of northern Kenya, came from sediments about 6 myr old and consisted of several jaw fragments with teeth, plus several partial postcranial bones. When described in 2001 by Senut, Martin Pickford, and colleagues, these fossils were given the name *Orrorin tugenensis* and were interpreted as the remains of an early hominid that had walked upright when on the ground while retaining some arboreal adaptations in its arms. The functional picture painted by Senut and colleagues was fairly well in line with expectations for a very early hominid, but it nonetheless rapidly became embroiled in controversy.

The dental material was not the problem: the upper canine described by Senut and colleagues was quite similar to specimens ascribed to *Ardipithecus*, if a bit blunter, and the molars were broader and satisfyingly thick-enamelled: well on the way to the grandly termed "postcanine megadonty" that was such a conspicuous characteristic of the australopiths. The problem lay in the postcranial bones, most specifically in the three pieces of thigh bone that provided the claimed evidence for bipedality. All consisted only of the proximal halves of the bone, and only one had anything remaining of the articular end. Essentially, the argument for bipedality had to rest on the bony architecture of the neck of the femur, where the weight of the body would have been transferred from the head of the bone to the shaft. The evidence for the type of weight transmission involved—which is distinctly different in quadrupeds and bipeds—is not unequivocally readable from the external form of the bone as preserved, at least not at present; and there is continuing argument over the currently available imagery of the bones' internal structure.

What particularly irritated the Middle Awash group, however, was the form of the early hominid family tree as inferred by Senut and Pickford. In this scheme the researchers sidelined *Ardipithecus* to a lineage that had ultimately led to the modern chimpanzee, and that had separated from the main hominid line at between 8 and 9 myr ago. A million years later, the lineage leading toward *Homo* split from another one that dead-ended in *Australopithecus* about 1.5 myr ago. *Orrorin* lay safely beyond this split, as the earliest identified unique ancestor of *Homo*. Especially given the rather scrappy nature of

the material from the Tugen Hills, this was a provocative view; and, given the severely linear notion of human evolution espoused by the Middle Awash group, it was bound to incur opposition from that quarter. It remains a minority view, though it has not been abandoned by its advocates.

Sahelanthropus

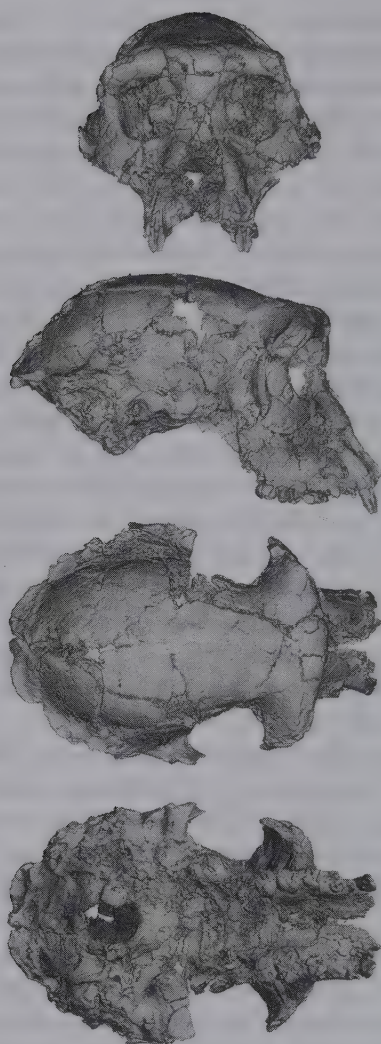
The dust had not even begun to settle on the *Ardipithecus/Orrorin* argument before what was perhaps the most remarkable contestant of all entered the “earliest hominid” stakes. Prior to the current millennium, virtually all early hominid fossils had been discovered either in South Africa or along the line of the great African Rift Valley, which bisects the continent into eastern and western portions. The existence of this remarkable tectonic and topographic feature had led Yves Coppens to propose his “East Side Story,” an attractive formulation whereby the doming-up of this structure along its length during the Miocene, in particular, had created a rain shadow to its east. According to this narrative, the rain forest to the west of the Rift had continued to harbor early apes, whose modern relatives—chimpanzees, bonobos, and gorillas—continue to flourish (or at least hang on) there to this day, while in the drying east the forest began to break up, forcing populations of hominoids to the ground and eventually leading to the emergence of the bipedal hominid family. There is something compelling to the human mind about simple cause-and-effect stories such as this, and of course the prediction from this particular scenario was that hominid fossils would not be found to the west of the Rift. This expectation had, of course, taken a bit of a battering from the 1995 announcement of *Australopithecus bahrelghazali*, the name given to a fragmentary hominid lower jaw found in the Republic of Chad, more than 1,500 miles to the west of the Rift! Nonetheless, the surprise was immense when, in 2002, a team lead by the French paleontologist Michel Brunet announced the discovery of a very early hominid cranium at Toros-Menalla, another site in Chad. The fossiliferous localities there lay in sandstones that could not be directly dated, but they contained a fauna (with riverine forest, woodland, and savanna components) that the team found to be closely comparable to Kenyan faunas dated to the 7.4- to 5.2-myr period. The researchers guessed an age of between 7 and 6 myr, and probably earlier rather than later in that span.

The hominid material was spectacular, consisting of a badly crushed cranium with most teeth broken, plus some mandibular fragments and isolated teeth, including a canine. The cranium was nicknamed “Toumaï,” and the assemblage was assigned to the new genus and species *Sahelanthropus tchadensis*. The whole thing looked a bit odd, not least because, while Toumaï’s braincase was extremely small, having contained a brain of only around 320–380 ml in volume, and was adorned at the back with a small sagittal crest, its face was flattish and very unlike the long face predicted for an early hominid. Indeed, it was not only unlike anything anyone had ever seen, it was unlike anything

anyone had ever expected to see. Commenting on Toumaï's announcement in the issue of the journal *Nature* in which it was published, the paleoanthropologist Bernard Wood expressed fairly typical astonishment that such an ancient hominid should depart so far in some major features from its presumed closest relative the chimpanzee; he also reflected paleoanthropology's collective surprise when remarking on its "mosaic" nature: the extraordinary combination of such a "primitive" skull rear with such "advanced" architecture of the face. "From the back," he wrote, "it looks like a chimpanzee, whereas from the front it could pass for a 1.75-million-year-old advanced australopith." It was such ruminations that governed his comment on the implications of the new find for the larger debate over the nature of early hominid phylogeny. In this debate, Wood pointed out, a "tidy" view (i.e., a linear one, such as that espoused by the advocates of *Ardipithecus*) was pitted against an "untidy" or "bushy" model that saw human evolution as a succession of mini-radiations. Supporting the untidy view, Wood saw in Toumaï "telling evidence" for an early "adaptive radiation of fossil apelike creatures that included the common ancestor of modern humans and chimpanzees." But what he did not see was any evidence that Toumaï was not actually a hominid, and it was left to Milford Wolpoff and a group of colleagues that included Brigitte Senut to come up with the suggestion that here was actually an "ape... with a powerful masticatory complex." Senut later suggested that it was actually a relative of the gorilla.

Apart from a minor spat that broke out between Brunet and one of his numerous coauthors of the original *Sahelanthropus* paper over some technical issues such as the identification of one of Toumaï's teeth, which had become detached, things rested there until 2005. In that year further material from Toros-Menalla was announced by the Brunet team. These new bits included two partial and rather badly damaged lower jaws, one of which included a smallish lower canine that was "consistent with a non-honing [canine-premolar] complex" (though the University of Pittsburgh's Jeffrey Schwartz pointed out that the canine in Toumaï's upper jaw would have occluded with a tooth much more pointed than this one was). The new finds, the authors concluded, "confirmed... the morphological affinities" of *Sahelanthropus* "with the hominid clade." Nonetheless, the most compelling reason to view Toumaï as hominid—and certainly a vital one—still remained the claim that in this cranium the foramen magnum was oriented downward, as in an upright biped. Wolpoff and colleagues, however, had questioned whether this was in fact so; and it was clearly true that, given the crushed condition of the skull, there was wiggle room here, either way.

The problem this presented was addressed in a contribution, published along with the report on the new material, by a team led by Christoph Zollikofer, of the University of Zürich. Zollikofer and colleagues took a computed tomography scan of the original Toumaï fossil, "virtually dissected" the broken skull into its major undistorted components on a computer screen,



Virtual reconstruction of the holotype cranium of *Sahelanthropus tchadensis*, in four views. Courtesy of C. Zollikofer and M. Ponce de Leon.

and then reassembled them in such a way as to minimize the displacement between them. The resulting three-dimensional model could then be transformed into a tangible replica of the undistorted skull by using a stereolithographic process originally developed for use by surgeons about to undertake tricky maxillofacial surgeries. The resulting replica of the cranium, as it would have been before postmortem distortion, offered a suite of features that not only tended to confirm the diagnosis of *Sahelanthropus* as a hominid, but that

also enhanced the probability that it was bipedal—which was the best that could be done, given the difficulty of *proving* bipedality from the skull alone.

Impressive as this technical feat was, it predictably enough failed to put an end to the argument. Wolpoff and colleagues returned to the fray in 2006, and several other paleoanthropologists also voiced doubts. The underlying problem, of course, was that nobody knew what an ancestral hominid “ought” to look like—which meant that geological age had become the most essential criterion. Because hominids are where it’s at, anyone finding a hominoid that lay in in the general time-zone of convergence of the ape and human lineages, and that didn’t look like a chimpanzee, was almost bound to interpret it as a hominid. Of course, this does not necessarily mean that *Ardipithecus*, *Orrorin*, and *Sahelanthropus* are not hominids in a strict phylogenetic sense, but it does mean that the criteria applied to them were not as rigorous as they might have been.

Perhaps this was unavoidable in the very nature of things; but certainly one reason why this rather questionable dynamic didn’t seem to bother paleoanthropologists very much was their expectation that, the closer in time to the ape–human split a fossil lay, the more “apelike” (for which read “chimpanzee-like”) it should look. A systematic search for diagnostic criteria to help in recognizing what was and was not a hominid thus somehow seemed less than urgent, particularly in light of the limited comparative base and the inherent difficulty of the task. In any event, by 2007 the ad hoc process of accretion of “earliest hominids” had resulted in a rather miscellaneous bunch of claimants for this distinction, with a rather diverse set of morphologies. Apart from presumed upright terrestrial locomotion, there was little if anything that united all of them, and one problem with uprightness as a defining characteristic for hominids was that, in all probability, more than one lineage of posturally erect arboreal hominoid might well have adopted bipedality on the ground once their ancestral arboreal habitat started to shrink.

Back to Kenya

At our current state of knowledge, then, the 4- to 7-myr time period remains a bit of a minefield for paleoanthropologists. Fortunately, though, beginning around 4 myr ago, we find ourselves on safer ground. For not long after *Ardipithecus ramidus* made its initial debut, another ancient claimant for early hominid status appeared on the scene. In 1995 Meave Leakey and colleagues reported finding dental, cranial, and postcranial specimens from northern Kenya that they allocated to the new hominid species *Australopithecus anamensis*. Some of the specimens came from localities at Kanapoi about 4.2 myr old; the rest came from exposures at Allia Bay about 3.9 myr old. Judging from the associated faunas, the Kanapoi hominids had inhabited a dryish bushland habitat, while the Allia Bay forms had lived along a river lined with gallery forest that had yielded to woodland away from the water. While quite



Upper and lower jaws of *Australopithecus anamensis* from Kanapoi, Kenya. Photos of casts by Sara Arias.

distinctive, the hominid remains from these sites were a great deal more reminiscent of *Australopithecus afarensis* than *Ardipithecus* was, and Leakey and her colleagues suggested that, with its “mosaic of primitive and derived features,” their new species was plausibly ancestral to *A. afarensis*. This placed *Ardipithecus* on a side line, as a “sister species to [*A. afarensis*] and all later hominids.”

One of the most exciting finds from Kanapoi was a broken tibia that preserved both extremities. Both the knee and ankle joint portions of the bone displayed features confirming that its possessor had walked upright. At last a firm indication that hominids had been up and walking on two legs terrestrially over 4 myr ago! And another characteristic of *Australopithecus anamensis* was of particular interest: one of the very few features that had been touted by White and colleagues as uniquely hominid was a reduction, compared to the apes, in the disparity between males and females in canine size. Samples of the earlier putative hominids were too small to allow determination of whether the other contenders showed such a difference; and although the known remains of *A. anamensis* were quite fragmentary, they were sufficient in number to show that the overall size range in this feature was modest.

In 1998 Leakey and her colleagues described further fossils from both Kanapoi and Allia Bay that they also ascribed to *Australopithecus anamensis*. They found in these specimens confirmation of the notion that *A. anamensis* was “demonstrably more primitive” than *A. afarensis*, and tied down the age of almost all the Kanapoi fossils to between 4.17 and 4.07 myr, placing them firmly in the time zone intermediate between *Ardipithecus ramidus* and

Australopithecus afarensis. They even reported that one first deciduous molar was “intermediate” in morphology between those two species. In a monograph published in 2001, the Kanapoi team ultimately backed away a little from this implication that their species was phylogenetically intermediate between *Ar. ramidus* and *A. afarensis*, although they did conclude that there “appears (sic) to be no apomorphies [derived features] precluding *A. anamensis* from ancestry of *A. afarensis*.” They also wavered a bit in the assignment of the more limited and less diagnostic Allia Bay materials to the same species as the Kanapoi fossils, although they continued provisionally to group the two assemblages. They noted that the reduced anterior dentition and thick molar enamel of *A. anamensis* suggested “a dietary shift towards tougher foods” from an “ape-like condition” that was still reflected in the structure of the fairly parallel-sided jaws, and they hazarded that “reduced canine sexual dimorphism,” in combination with “apparently high levels of body mass dimorphism,” might indicate “a unique social system characterized by high levels of male-male competition that did not involve the use of canine teeth.” As a result, they correlated the acquisition of hominid bipedality with changes both in “diet and/or social behavior,” while also observing that probably all of these changes were ultimately environmentally driven.

More Entrants

For a while, Kanapoi and Allia Bay remained the only sites from which *Australopithecus anamensis* was known—although in a press conference in 2005 Haile-Selassie announced the discovery of a skeleton at a place called Mille in Ethiopia’s central Afar Depression. This was just under 4 myr old, and thus in the same time range. However, in 2006 Tim White and the Middle Awash team published a suite of fossil fragments, part of a woodland fauna from the site of Assa Issie, a little to the west of Aramis. Dating to around 4.2–4.1 myr, hence almost exactly contemporaneous with the Kanapoi finds, the hominids from Assa Issie were assigned to *A. anamensis*. To the Middle Awash group, these new *A. anamensis* specimens clinched the position of this species as the middle segment of a steadily evolving lineage leading from *Ardipithecus ramidus* to *Australopithecus afarensis*, the highly distinctive features of the latter having emerged in a 200 kyr interval. They did consider the alternative possibility that both had been descended from an *Ardipithecus*-like ancestor that existed earlier in time than the Aramis population (which would then have represented “a relict species in an ecological refugium”), but rejected it.

Whatever the case, much like the Kanapoi group, White and colleagues came to the conclusion that the “diagnostic... morphology of *Australopithecus*” (involving expansion of the chewing teeth and associated changes in their supporting structures) had appeared by 4.2 myr ago, and beyond this that this new dental structure indicated “a more heavily chewed diet of tough and

abrasive items than that of *Ardipithecus*." One possibility this dietary shift raised was that of an "ecological breakout," with "intensified exploitation of more open...habitats." Given the general faunal similarities between Aramis and Assa Issie, however, they concluded that the Assa Issie population of *Australopithecus anamensis*, at least, had continued to exploit the ancestral habitat, albeit presumably in a rather different way. And they suggested that the tendency toward massiveness in the dentition announced by *A. anamensis* (*Orrorin* and *Sahelanthropus* played no part in this analysis) had continued to dominate events in hominid evolution for several million years, right up until the emergence of the genus *Homo*—after the invention of stone tools.

The notion that *Australopithecus anamensis* had evolved directly into *A. afarensis* received support in 2006, from an analysis published by a group of authors that included members of both the Kanapoi and Hadar groups. These scientists took four time-successive hominid samples (from Kanapoi, Allia Bay, Laetoli, and Hadar) and subjected them to quantitative phylogenetic analysis using some twenty character states. This analysis showed that each sample shared derived states only with samples from later in time, which is what you would expect to find in a lineage modifying over time. And while it is also at least compatible with multiple speciations, the conclusion was that here was *prima facie* evidence for "anagenetic" change within a single lineage. The authors did note, however, that "evidentiary support for the hypothesis is weakest" in the gap between Allia Bay and Laetoli, i.e., precisely the interval separating *Australopithecus anamensis* and *A. afarensis*. And in a review of hominid morphologies published in 2005, Jeffrey Schwartz and I pointed out that the range of detailed dental morphologies present in the entire sample of hominids from the 4.2- to 3.0-myr period was rather greater than had generally been appreciated.

Hadar Again

While all this was going on, knowledge of *Australopithecus afarensis* itself was increasing apace, with renewal of work at Hadar by the Institute of Human Origins. A spectacular find was made by Yoel Rak in 1992 of a large skull, presumed male, that was broken into many pieces but that was complete enough to be reconstructed into the first *A. afarensis* cranium that was not cobbled together from bits of different individuals.

It received the number AL 444-1, and along with various less consequential specimens it was described in *Nature* in 1994 by Bill Kimbel and colleagues, who found that it supported the unity of *A. afarensis*. Ten years later Kimbel, along with Rak and Don Johanson, published a splendid monograph that described 444-1 in detail and summarized the highly fruitful results of fieldwork at Hadar in the years from 1990 to 1994 and from 1999 to 2001. Among the many specimens recovered in these field seasons (though too late, alas, to be described in the monograph) was a smaller and even more complete



Right side view of cranium of *Australopithecus afarensis*, AL 444-1, from Hadar, Ethiopia. Photo by and courtesy of W. Kimbel/IHO.

skull (AL 822-1), presumed to be female. The monograph itself gave Kimbel and his colleagues the opportunity to reflect on the very large sample of hominids that had been collected at Hadar over more than a quarter-century. And in it they reaffirmed their belief that the entire very large hominid sample from Hadar represented the same species.

As to whether the Laetoli and Hadar samples belonged together, they were very slightly more equivocal. They did see some significant differences, especially in jaw morphology, between the Laetoli and Hadar samples. And while they declined to separate the two samples into different species (which would have created a tricky nomenclatural situation, for the Tanzanian type material would have had to keep the name *afarensis*), they did anticipate their later conclusion by observing that those characters that set Laetoli apart from Hadar might indicate intermediacy with *A. anamensis*. Alternatively, they suggested that Laetoli might represent a “distinct clade in a sister-species relationship with *A. afarensis*,” veering toward a conclusion that Jeffrey Schwartz and I mooted on different grounds in 2005. This was that significant morphological differences existed between the Laetoli and Hadar hominids in the jaws and teeth—although a major difference was that, in addition, we also found dental evidence for more than one morph in the Hadar sample. Interestingly, the inference that different hominid species were represented by the fossils from Hadar and Laetoli was also in line with the notion, first raised by the anatomist Russell Tuttle in the 1980s and elaborated by the English paleo-anthropologist Will Harcourt-Smith in 2007, that the Laetoli footprint trails could not have been made by the hominid whose foot bones had been found at Hadar. The Laetoli footprints show clear evidence of a longitudinal arch, a

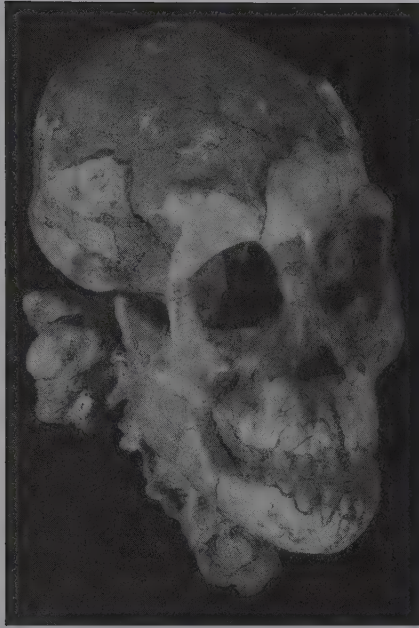
feature lacking in the Hadar foot, and the proportions of the feet also appear to have differed in the two cases.

Having decided in favor of the unity of *Australopithecus afarensis*, Kimbel and colleagues proceeded to consider the place of this species in hominid phylogeny. And a series of quantitative phylogenetic analyses produced the conclusion that *A. afarensis* was the sister taxon of all other hominids, indeed that this species was basal to the entire hominid radiation. This result was perhaps unsurprising because, for want of adequate material to allow the kind of detailed comparisons they were making among the *A. afarensis* samples, the authors had excluded all of the other early hominids: *Ardipithecus ramidus*, *Australopithecus anamensis*, and so on. They also compiled lists of morphological features present in the various later taxa, and they found *Australopithecus afarensis* to be generally primitive compared to later hominids, lacking in derived features that might exclude it as the ancestor of the later hominid radiation.

Sporadically throughout the history of study of *A. afarensis*, the suggestion had been made that the species harbored various similarities—and hence some phylogenetic connection—to the robust australopiths; and Kimbel and colleagues listed seven such features. However, at that time they considered all of these to be “nonhomologous,” i.e., independently acquired, and not indicative of evolutionary relationship. At least one of the coauthors of the monograph subsequently changed his mind, however. Looking at the mandible of the newly discovered AL 822-1 skull, Yoel Rak identified a condition of the ascending ramus of the mandible (basically, a constriction of the mandibular notch) that matched what was seen in robust australopiths (and, presumably independently, in gorillas), but was paralleled in no other hominid or great ape. To his mind this tipped the balance, and in 2007, with two colleagues, Rak published the conclusion that *A. afarensis* was a probable ancestor (or at least sister) of the robusts. And given that the other australopiths and *Homo* all exhibit the primitive ramal condition, there was no way *A. afarensis* could have been ancestral to them as well.

A Tale of Two Skeletons

Although major hominid prospection at Hadar is currently discontinued, largely because the rate of collection has exceeded the rate of erosion, the drama is not over. The Dikika area that lies just across the Awash River also contains rocks of the Hadar Formation and is also yielding fossils. In 2005 Zeresenay Alemseged of the California Academy of Sciences, together with a group of colleagues that included Kimbel, reported finding hominid remains there for the first time. These came in the form of a partial mandible attributed to *Australopithecus afarensis* and dated to about 3.4 myr, the age of the First Family. But that was just the beginning. In late 2006 *National Geographic* magazine carried a feature story on a most remarkable find from Dikika: the



The infant hominid skull from Dikika, Ethiopia. *Courtesy of Zeresenay Alemseged.*

skeleton of an infant female, who died some 3.3 myr ago at about the age of three. This amazing specimen makes up for her immaturity by being far more complete than Lucy, with fingers, a foot, and a complete torso. She even preserves her hyoid, the bone in the throat that supports the voicebox. Her brain, at about 330 ml, is equivalent in size to that of a chimpanzee of similar age. Cleaning away the hard sandstone matrix is a slow process, but once the task is completed this skeleton promises to tell us a great deal more than we know now about the kind of creature *Australopithecus afarensis* was.

Something very similar can be said for a skeleton of approximately the same antiquity that is currently being excavated in Member 2 of the classic South African site of Sterkfontein. The story of the discovery of this skeleton, technically catalogued as StW 573 but more widely known by its popular name of "Little Foot," is as remarkable as any in paleoanthropology. In 1994 and 1997 Ron Clarke, whom we have encountered before, ran across a dozen foot and lower leg bones from Sterkfontein 2 while rummaging through boxes of bones dynamited out of the "Silberberg Grotto" section of the site many years earlier. These had been misidentified and forgotten about, but Clarke recognized that they belonged to a species of *Australopithecus*, and he also saw that a piece of distal right tibia had been freshly broken off. Surmising that the rest of the skeleton might thus still be in the rock matrix out of which the tibia had been blasted, he asked two of his associates, Stephen Motsumi and Nkwane Molefe, to return to the gloomy, cavernous grotto and to try to match



In situ view of the skull and left upper arm of the "Little Foot" *Australopithecus* skeleton from Sterkfontein Member 2, South Africa. *Courtesy of Ron Clarke.*

the broken tibial shaft with anything visible in the cave wall. Miraculously, on July 3, 1997, within two days of this request to find a needle in a haystack, they located the match they sought. Subsequent excavation revealed that most of the skeleton, including the skull, the entire left hand, and a rather crushed pelvis, was present.

Apparently, some 3.3 myr ago (as paleomagnetically dated from the surrounding flowstones; this is currently believed to be the most reliable of several different age estimates) the unfortunate individual somehow fell into a cavity in the limestone and found itself unable to escape. Unmolested by scavengers (though somewhat disassembled by earth movements), its body remained

intact in the cavity, which ultimately filled up with rubble and flowstone. The calcite-cemented matrix is fiendishly difficult to remove, and working conditions inside the cave are very difficult, so at this writing the skeleton is still under excavation, but already it is clear that, whatever it is, this is not a typical Sterkfontein *Australopithecus africanus*. Interestingly, Clarke reported at the end of 2002 that the arms are not particularly long compared to the legs, and that the hand is humanlike in having a relatively long thumb and short fingers. The creature was, he believed, “a climber in the trees...and bipedal on the ground.” Further, he concluded that the specimen provided no particular support for the notion that hominids and chimpanzees are each other’s closest relatives, largely because of a total absence of knuckle-walking morphologies in the left hand of StW 573, the only complete australopith hand known. This specimen is set to become a major focus of discussion in paleoanthropology once it is finally freed from the enclosing matrix.

Interestingly, another initially misidentified Sterkfontein specimen, this one from the later Member 4, has also recently contributed to the debate over early hominid locomotion. StW 431, a partial pelvis, undeformed on the right side, was described in 2003 by Clarke and his colleague J. M. Kibii, and clearly shows the laterally flaring morphology that was described by the Swiss paleoanthropologist Peter Schmid in 1983 for the “Lucy” pelvis of *Australopithecus afarensis* (in contradiction of a much more humanlike earlier reconstruction of the same pelvis by Owen Lovejoy and colleagues). StW 431 also flares much more than the classic reconstruction of the Sts 14 pelvis from Sterkfontein 4 made by John Robinson back in the 1950s. Overall, Kibii and Clarke found that the new specimen supported the conclusion, initially reached by Randy Susman and colleagues in 1984, that the lateral orientation of the iliac blades “is well suited for a part-time climber and part-time terrestrial biped.” If so, then at least part of the adaptation later coopted for terrestrial bipedalism may have been initially acquired in an arboreal context.

A New “Robust”

The 1990s also saw the first discovery, for as long as most people could remember, of an entirely new important australopith site in South Africa. This was the locality at Drimolen, some 4 miles north of Sterkfontein, which was discovered by the geologist André Keyser in July, 1992. The first hominid fossil, a partial skull, showed up in 1994, and several dozen additional hominids (most of them isolated teeth) have since been found by Keyser and his coworkers, notably a French group including José Braga and Dominique Gommery. Although the nonhominid fossils from Drimolen do not include any highly time-sensitive species, Keyser and colleagues reckoned in a review published in 2000 that an age of between 2.0 and 1.5 myr is reasonable. Perhaps because of this latish date (although also because of large cheek tooth size), and despite the lack of any “consistent and exclusive pattern of metrical



Three-quarter view of the DN 7 skull from Drimolen, South Africa, as restored by G. J. Sawyer. *Photograph of cast by Jennifer Steffey; 1-cm scale.*

and morphological similarity to either the Swartkrans and Kromdraai samples," the Drimolen group has allocated the bulk of the hominid fossils from the site to *Paranthropus robustus*. However, it remains true that the DNH 7 skull from Drimolen, heralded in 2000 as "the most complete australopithecine cranium and mandible to date," contrasts strongly in its tall and narrow orbital and overall facial structure with anything known from Swartkrans or Kromdraai; and although there are comparisons to be made with specimens from Swartkrans in the upper dentition, these are, as Jeffrey Schwartz and I pointed out in 2005, no more striking than those to be made with at least one specimen from Sterkfontein. Overall, what the hominids from Drimolen do most dramatically is to emphasize the increasing difficulty of squeezing the fossils from the South African australopith sites into the limited number of traditional categories. Additionally, and also by comparison with Swartkrans, some of the hominid teeth from Drimolen have been attributed to *Homo*, thus complicating the situation yet further.

At the other end of the South African australopith time spectrum, Ron Clarke and colleagues reported in 2003 on hominid finds made in the Jacovec Cavern, another part of the extensive Sterkfontein cave system. The hominids concerned consisted of parts of a braincase and some teeth and postcranial bones (one a rather chimpanzee-like clavicle), which they attributed to *Australopithecus* but did not assign to species. Dating was, however, by a very new method involving cosmogenic nuclides of aluminum and beryllium, which gave almost identical ages for Jacovec and Sterkfontein Member 2 of about 4.2–4.0 myr. Initially the group took this as evidence for an even greater age for

the Little Foot skeleton than they had initially believed; subsequently, though, they have reverted to the earlier 3.3 myr date for StW 573, and this may indicate the necessity of reconsidering the very ancient date for Jacovec as well.

Isotopes Again

Not only new fossils, but new methods, enlivened our view of the australopiths during the 1990s. Notable among these was the application of stable isotope studies to questions of australopith diet. As we have seen, in the case of more recent hominids such as the Neanderthals, the isotopes of choice have been of nitrogen. For studies of the australopiths, isotopes of carbon have been favored. From an isotopic point of view, plants fall into two categories. Most fix atmospheric carbon dioxide using what is known as the C_3 photosynthetic pathway. Such plants, which include trees, shrubs, and temperate grasses, are relatively depleted in the ^{13}C isotope. The rest, mostly tropical and savannah grasses, follow the C_4 pathway and, because they fractionate atmospheric carbon isotopes less strongly, are higher in their ^{13}C values. Since animals do not greatly fractionate carbon isotopes at all, they maintain the isotope ratios present in the plants they eat: a fact that provides an obvious clue to their diet. The collagen that is preferably used in isotopic studies of more recent mammals degrades fairly rapidly, limiting the use of collagen analysis to the past few hundred thousand years. However, as demonstrated in 1987 by Julia Lee-Thorpe and Nikolaas van der Merwe at the University of Cape Town, it turns out that carbonate ions containing ^{13}C are durably incorporated into the inorganic structure of the bones and, particularly, of the teeth. As a result, using enamel carbonate from fossil teeth, Lee-Thorp and colleagues were able to suggest in 1994 that robust australopiths from Swartkrans, believed at the time on the basis of their massive grinding molar apparatus to be strictly vegetarian, were actually fairly omnivorous. This is because the isotopic results showed a mixture of both C_3 and C_4 foods, which implied an animal component to the diet because the robusts were clearly not grazers, and the most likely source of the C_4 component was thus grazing animals.

Latterly, in collaboration with her younger colleague Matt Sponheimer, Lee-Thorp has gone on to enlarge greatly the range of stable isotope studies of australopiths in relation to diet. When she began working in this field in the late 1980s it was generally thought (in dramatic contrast to Raymond Dart's ideas of a half-century earlier) that *Australopithecus africanus* existed on chimpanzeelike diet that consisted principally of fleshy fruits and leaves, while the robusts used their massive molars to process such tough stuff as nuts and grains. This notion owed a lot to the English paleoanthropologist Clifford Jolly's seminal "seed-eater" model, developed in the late 1960s. This saw morphological contrasts, similar to those separating gracile and robust early hominids, between the more generalist hamadryas baboons on the one hand, and the closely related and sympatric geladas that subsisted on a diet of

grass grains, corms, and rhizomes, on the other. But since the chimpanzee-like diet carries a C_3 signature while the geladalike one is C_4 , if this were the case the two kinds of australopith should carry distinctive isotopic signals, and this turned out not to be so. What's more, the isotopic signatures of both hominid groups were very different from those of their C_3 -consuming contemporaries. Across all the australopith sites in South Africa, there emerged a fairly consistent signal that indicated a 40% or so C_4 diet for hominids of all kinds—irrespective of microhabitat.

So where was all this C_4 coming from? One possibility was directly from grasses and sedges, the primary source. But while Lee-Thorp and Sponheimer acknowledged this as a local possibility, for a host of reasons they considered it implausible as a general pattern. Instead, they opted for animals (in the large sense, including insects, reptiles, and all kinds of invertebrates—and in fact, one recent suggestion is that the broad, flat teeth of such hominids as *Paranthropus boisei* were ideal for cracking arthropods and small crabs). The strong C_4 signal found in the hominids could not have come from favorite chimpanzee prey such as blue duiker and colobus monkeys, for these animals exist on C_3 diets. More likely, Lee-Thorp and Sponheimer suggested, it came from small-bodied grass eaters such as hyraxes, or from the young of larger-bodied grazers. Arthropods and termites were another suggestion. The current bottom line is, though, that right now we can't know for sure exactly what the australopiths were eating; all we have is the very strong suggestion that the strong C_4 signal ubiquitous in South African australopith diets was animal derived. Still, this is very important, because the adoption of a high-quality diet of this kind was almost certainly an absolutely essential prerequisite to the expansion of the energy-hungry hominid brain that was about to take place.

New Australopiths from Ethiopia

In Ethiopia, too, the 1990s saw the discovery of intriguing new australopith specimens. One of them, grandiosely billed as “the first skull of *Australopithecus boisei*” because a lower jaw was associated with the cranium although much of the face is missing, came from the 1.4-myr-old site of Konso, in southern Ethiopia. Along with the hominid skull, described in 1994 by the Japanese paleoanthropologist Gen Suwa and colleagues, the site also yielded various smaller hominid bits, assorted mammalian fossils, and Acheulean tools. Although the specimen has only been preliminarily described and illustrated and is not available for general study, the species allocation to *Australopithecus boisei* seems on the face of it reasonable, at least in a broad sense (the caveat being that, as Jeffrey Schwartz and I pointed out in 2005, the type specimen of *Paranthropus boisei* from Olduvai differs distinctly in the morphology of the upper face from Richard Leakey's classical KNM-ER 406 exemplar from East Turkana, while closely resembling the distinctively different ER 23000 frontal



The robust australopith cranium from Konso, Ethiopia. *Courtesy of Gen Suwa.*

from the same region—and it is this this element precisely that is missing from the Konso specimen).

Possibly less easy to sustain is the claim advanced by Suwa and colleagues that the Konso specimen, as the latest known of the “robusts,” is also the most “advanced.” It certainly appears to have some features that are not typical of older specimens allocated to *Paranthropus boisei*, but the authors’ claim that they reflect a linear evolutionary trend is harder to demonstrate. A comprehensive description of this important specimen is eagerly awaited.

Farther north in Ethiopia, in 1999 the Ethiopian paleoanthropologist Berhane Asfaw and a group of colleagues described a new species of *Australopithecus*, *A. garhi*, from 2.5-myr-old lake-margin deposits in the Bouri Formation of the Middle Awash region. The principal specimen of this new hominid was a partial cranium gracefully dubbed BOU-VP-12/130; but other elements, including some teeth, a mandible, and possibly postcranial bones, were also recovered and attributed to the same form. According to the describers this specimen, which is not available for independent analysis, is principally distinguished from *Australopithecus afarensis* by its very large postcanine dentition, and from the robusts by large anterior teeth. As hinted by Kimbel and his colleagues in their 2004 analysis of the *A. afarensis* cranium, however, there does not appear to be much about the face or what is left of the skull vault to distinguish it from the latter. And in regard to the teeth, Schwartz and I noted in 2005 that, on the basis of the few available photographs, the closest match to the *A. garhi* palatal dentition seemed to be in a subset of the *A. afarensis* assemblage from Hadar. Whether these Bouri fossils deserve

their separate species identification thus still remains up in the air. Asfaw and his colleagues were reluctant to allocate the Bouri postcranials definitively to *A. garhi*, but they did note that the fossils indicated a rather long humerus compared to the femur, implying that the elongation of the lower limb that characterized later forms had not yet occurred in the hominid concerned.

For many years paleontologists had fretted that nothing convincingly intermediate between the australopiths and the earliest well-defined *Homo* was known; and Asfaw's group pointed out that their *A. garhi* was in the right place and right time to occupy a transitional position. Further, they believed that "nothing about its morphology would preclude its occupying this position." So while both admitting that there was no way of knowing whether *Homo* ultimately descended from a member of the southern or the eastern African early hominid radiations, and acknowledging the difficulties of recognizing early fossils of *Homo* in the absence of any agreed definition of the genus, they were prepared to speculate that *A. garhi* was, somehow, at least close to the australopith-*Homo* transition. So much for where *A. garhi* was going; but when initially describing the Bouri material, Asfaw and colleagues, while hinting at close resemblances between *A. garhi* and *A. afarensis*, refrained from placing the two in a straight line of descent. However, by 2006 the group had evidently lost its reservations on this matter, for in their publication describing the new material from Assa Issie they were confident enough to refer directly to an *A. anamensis*→*A. afarensis*→*A. garhi* lineage.

Perhaps even more interesting than the *Australopithecus garhi* fossils themselves was their context. Bouri is not far from Gona, whence the earliest (2.6-myr-old) stone tools had been reported in abundance by the Ethiopian archaeologist Sileshi Semaw and colleagues in 1997. In the slightly younger Hata beds of the Bouri Formation, in which the *A. garhi* fossils had been found, tools themselves were rare, possibly because of a shortage of naturally occurring suitable materials. But, at a couple of localities, mammal bones were found that showed signs of battering and cut marks from stone tools. This was unquestioned evidence of hominid tool-using activity; and although there was no direct association between the cut-marked bones and the fossils of *A. garhi*, this species was the only hominid known from the area. For the time being, then, it seems reasonable to suppose that it was individuals belonging to *A. garhi* who made and used the tools; if this is the case, it is a powerful reason for supposing that stone tool making was invented not by members of the vaunted genus *Homo*, but by small-brained and archaically proportioned australopiths.

Homo Revisited

As Asfaw and colleagues well knew, just what our genus is remained a difficult question in the absence of any adequate morphological definition that would help us to recognize its early members. Even more keenly aware of the problems were the British paleoanthropologists Bernard Wood and Mark Collard.



The AL 666-1 palate from Hadar, Ethiopia. *Photo by and courtesy of W. Kimbel/IHO.*

In 1999 they revisited the issue of recognizing early *Homo* and concluded that “conventional criteria for allocating fossil species to *Homo* [are] either inappropriate or inoperable.” In a broad-ranging review, they presented a new algorithm for recognizing membership in *Homo* involving the demonstration that any candidate species 1) is more closely related to *H. sapiens* than it is to the australopiths; 2) has a body mass closer to *H. sapiens* than to the australopiths; 3) has reconstructed body proportions that match those of *H. sapiens* more closely than those of the australopiths; 4) has a postcranial skeleton consistent with modern humanlike bipedality (and limited climbing abilities); 5) has teeth and jaws closer in size to *H. sapiens* than the australopiths; and 6) shows a modern humanlike extended growth and development life phase. Applying these rough-and-ready criteria to the hominid fossil record, they found at least two species that did not meet them: *Homo habilis* and *H. rudolfensis*. As a result, they concluded that anything then known that was more “primitive” than *Homo ergaster* had to be excluded from *Homo* if the genus was to make morphological and phylogenetic sense. By implication, this also included everything in the 2.5- to 1.8 myr range that had been allocated to “early *Homo*” by authors whose species-recognition nerve had failed them. Bravo! But then they suggested that the two species *habilis* and *rudolfensis* should be transferred to *Australopithecus*—despite acknowledging that, while tidying up *Homo*, this would make *Australopithecus* even messier than it already was. Clearly, the paleoanthropological world was not yet ready for new genera.

As a result, the roster of “early *Homo*” specimens continued to mount. In 1996 and 1997 Bill Kimbel and colleagues described a fossil hominid palate (AL 666-1) from levels at Hadar that, at around 2.3 myr old, were younger than the classic 3.4- to 3.0-myr-old *Australopithecus*-yielding sediments



The UR 501 mandible from Uraha, in Malawi, that has been attributed to *Homo rudolfensis*. Courtesy of Tim Bromage.

of the region. These levels also yielded yielded Oldowan-type stone tools, in closer association with the fossils than was the case at Bouri. Since the well-preserved palate “showed unambiguous affinities with early representatives of the *Homo* clade,” Kimbel and colleagues allocated it to *Homo* aff. *H. habilis*, meaning that they believed its closest resemblances lay with the latter species. Nonetheless, in 2005 Schwartz and I pointed out that this specimen “possesses a very primitive and *Australopithecus*-like configuration of the nasoalveolar clivus relative to the palate,” quite unlike what is seen in members of the genus *Homo* as restricted by Wood and Collard. We also noted quite close dental resemblances to the Bouri *A. garhi* palate, to which AL 666-1 lies fairly close in both time and geography. As a result, we saw little justification for excluding the Hadar specimen from the *Australopithecus afarensis* sample. As with virtually all of the specimens in the 2.5 to 2.0 time frame that have been allocated to “early *Homo*,” the case is not yet demonstrated for recognizing evidence here of our own genus at this very early stage.

Another hominid palate with a complete if worn upper dentition was reported from upper Bed I at Olduvai Gorge in 2003 by a group led by Rutgers University archaeologist Rob Blumenschine. This one was about 1.8 myr old, was found with Oldowan stone artifacts and cut-marked bones, and predictably enough was allocated by its finders to *Homo habilis*. The researchers

noted that their specimen had “strong affinities” to the penecontemporaneous but edentulous KNM-ER 1470 from Koobi Fora to the north; but though its tooththrows are about the right size and shape to provide the missing teeth for the *Homo* (or *Australopithecus*) *rudolfensis* holotype, it is also fair to note not only that, as Schwartz and I concluded in 2005, the very incomplete and eroded ER 1470 is very indeterminate and inadequate as a type specimen, but that the teeth in the new Olduvai palate, OH 65, worn as they were, seemed to fit well with those of the KNM-ER 1813 and KNM-WT 15000 crania.

An additional specimen allocated to *Homo rudolfensis* was the UR 501 mandible described from the Uraha site in Malawi in 1993 by the German paleontologist Friedemann Schrenk and his colleagues. These authors made their determination on the basis of the similarities they perceived to the KNM-ER 1802 mandible that had been recovered from Koobi Fora many years earlier, but sadly the teeth in the new specimen are very worn, and a definitive allocation is hard to make. Just what—if anything—*Homo rudolfensis* is remains for the moment anybody's guess. Less doubtful is the partial temporal bone that was described in 1992 from the 2.4-myr-old site of Chemeron in Kenya's Baringo Basin. This was described in 1992 as the earliest “securely known” member of the genus *Homo*, but in 2005 Schwartz and I found it to be a close match for its counterpart in the KNM-WT 17000 cranium of *Paranthropus aethiopicus*. All in all, at the time of writing virtually all claims for “early *Homo*” over 2 myr old are looking fairly precarious, strongly supporting the approach to recognizing our genus advocated by Wood and Collard.

In 2001, paleoanthropological resistance to the multiplication of genera within the hominid family began to crack when Meave Leakey and colleagues bravely proposed the new genus *Kenyanthropus* to contain a 3.5-myr-old cranium (KNM-WT 40000) and 3.3-myr-old partial maxilla that were recovered from the Lomekwi and Topernawi drainages, respectively, both to the west of Kenya's Lake Turkana. A couple of partial mandibles that had previously been allocated to *Australopithecus afarensis* were also assigned to the new taxon. Comparable in cranial size to *A. afarensis* and *A. africanus*, the new form was given the species name of *K. platyops* (“flat-faced Kenyan man”) to reflect the flatness of the cranium's midfacial profile. Leakey and colleagues considered the facial structure of *K. platyops* to be more derived than that of *A. afarensis*, and that it was yet more primitive in certain other cranial features; they concluded that it provided evidence for a “taxonomically more diverse Pliocene hominin record” than had been previously recognized. Further, from the flatter face they inferred masticatory changes suggesting a “diet-driven adaptive radiation” among hominids of the 3- to 4-myr period. They felt it conservative to include all of their material within a single species, and at the same time they saw the necessity of creating a new genus since none of their new material fit at all comfortably within any genus then commonly recognized.

Still, Leakey and colleagues perceived similarities in facial structure between their *Kenyanthropus platyops* and the 1.5 myr younger KNM-ER



The holotype cranium (KNM-WT 40000) of *Kenyanthropus platyops* from Lomekwi, Kenya. Photograph by Fred Spoor; ©National Museums of Kenya. Courtesy of Meave Leakey.

1470, the type of *Homo rudolfensis*, although they also saw more “primitive” features in the morphology of the nasal region and cranial vault of the former. The similarities, they thought, indicated a phylogenetic relationship between the two; accordingly they proposed that, instead of being transferred as Wood and Collard had recommended to *Australopithecus*, the later form should be recognized as *Kenyanthropus rudolfensis*. These conclusions were promptly attacked by Tim White, who in 2003 strongly questioned the conclusion that the new material indicated diversity among hominids of the period in question. Instead, he suggested that the peculiarities of morphology in WT 40000 were in reality the result of postmortem distortion and that, to the extent that they were real, they constituted no more than minor variations of mere subspecific importance. As an expert on distortion, his views demanded attention; certainly the cranium showed a pattern of cracking of the bone and infiltration of sediment into the cracks. However, as Jeffrey Schwartz pointed out in response to White’s observations, the added sediment was fairly evenly distributed throughout the cranium, whose basic proportions would therefore have remained unaffected. Most paleoanthropologists, it seems, have accepted Leakey and colleagues’ conclusions without major demur.

Prospects

Although paleoanthropologists currently have a tendency to look back on the years between 1959 and 1984 as the Golden Quarter-Century of hominid fossil discovery, the past two decades have in their own way been equally rewarding. This applies not only to the earlier phases of hominid evolution from Toros-Menalla to Lomekwi to Dmanisi, but also to the later phases, including the increasingly hot issue of the origin of *Homo sapiens* itself. As the fossil record continues to grow, as dating methods are refined, and as new approaches unimaginable today become available, we can expect the long story of hominid evolution to become clearer—or at least we can hope that it will. Meanwhile we have to bear in mind, among other things, that the emergence of *Homo sapiens* is the most recent major event in the evolution of our lineage and that this fact has its downside as well as its advantages. Among the advantages is the rather large number of sites and fossils known from the period following about 100 kyr ago; but our close perspective also forces us to look at the picture in much finer grain than at any comparable earlier event in the human fossil record. Speciation is not a simple process (or miscellany of processes), and what little we know about it doesn't predict much about what we should expect to see in terms of anatomical evidence. Testing alternatives is thus not easy at the best of times; and it is most difficult of all when we are working with a lot of widely scattered and frequently fragmentary fossils.

Perhaps this is not the most satisfactory of all notes on which to end a story; but as we arrive at the state of our knowledge today, after looking at how it was sometimes painfully acquired over the last couple of hundred years, we have to bear in mind that the long soap opera of human emergence is a story that will never end as long as *Homo sapiens* persists on Earth. And any retrospective account has necessarily to stop in full spate, as it were, in the midst of a host of unresolved subplots and questions. I don't pretend that what you have read in this book is objective history in the strictest sense; it is simply the perception of one active practitioner of the science of paleoanthropology. But I do hope that it will have helped to produce some perspective on the state of play today. As I said right at the beginning, what we think today depends very largely on what we thought yesterday. If the entire human fossil record were to be discovered tomorrow and to be studied by experienced paleontologists who had developed their skills in the absence of any preconceptions about human origins, I am pretty sure that (after the inevitable bout of intellectual indigestion) a range of interpretations would emerge that is very different from what is on offer now.

CHAPTER 19

So, Where Are We?

Given the wealth of fossils, technologies, and interpretations on offer, it's a tall order to encapsulate the diverse field of paleoanthropology as it exists today. But if you've read this far, you're already familiar with the most important constituents of the human fossil record and with the principal interpretations of them that have been made. In this final chapter what I can most usefully do by way of summary is, I think, to change gear, and to follow my own advice and review the evidence for the past of our species (rather than the ways in which that evidence has been interpreted) by advancing from the (relatively) simple to the complex. This perforce means starting at the most basic level of analysis: species diversity in the human fossil record. It should by now be abundantly clear to everyone that hominid evolution has not been a straightforward story of a single gradually modifying lineage, a lineage battling its way through time, with the help of natural selection, from primitiveness to perfection. The story has been much more complex than that, and vastly more interesting. It has been a saga of constant evolutionary experimentation, of restless exploration of the many ways in which it is evidently possible to be a hominid.

As a result, hominid history has been an epic of new hominid species emerging, doing battle in the ecological arena and, more often than not, going extinct after wildly varying tenures. And before you can begin to work out the relationships among all of those extinct human relatives and figure out how they participated in and were shaped by the physical environments and ecological communities of their day, it is obvious that the most fundamental requirement is to have a reliable operating notion of what those species were. In these concluding pages I will thus briefly review this issue, before proceeding to outline a scenario of human evolution that focuses on something that has so far received no greater attention in this book than it has in paleoanthropology generally: the matter of what we can reasonably infer about how we came to possess the extraordinary and totally unprecedented cognitive powers that make us unique in the living world.

Systematics—The Key to Understanding the Hominids

We've already seen that the nitty-gritty of alpha taxonomy has not traditionally been paleoanthropologists' strongest suit. Partly this has been due to the multiple difficulties, both theoretical and operational, that are inherent in the exercise itself, especially within such a closely-knit group; but it also results from a widespread feeling that taxonomists are "just arguing about names" and that the really interesting questions lie elsewhere. Well, it is certainly true that systematics is not to everyone's taste. But it is much more significantly true that everything else we do in paleontology is underpinned by our systematics and that, if we get it wrong, everything else that we do will be compromised. Quite simply, you'll never understand the play if you don't know who the actors are; and paleontologists should at least be uneasy that estimates of the total number of extinct hominid species continue to vary so widely.

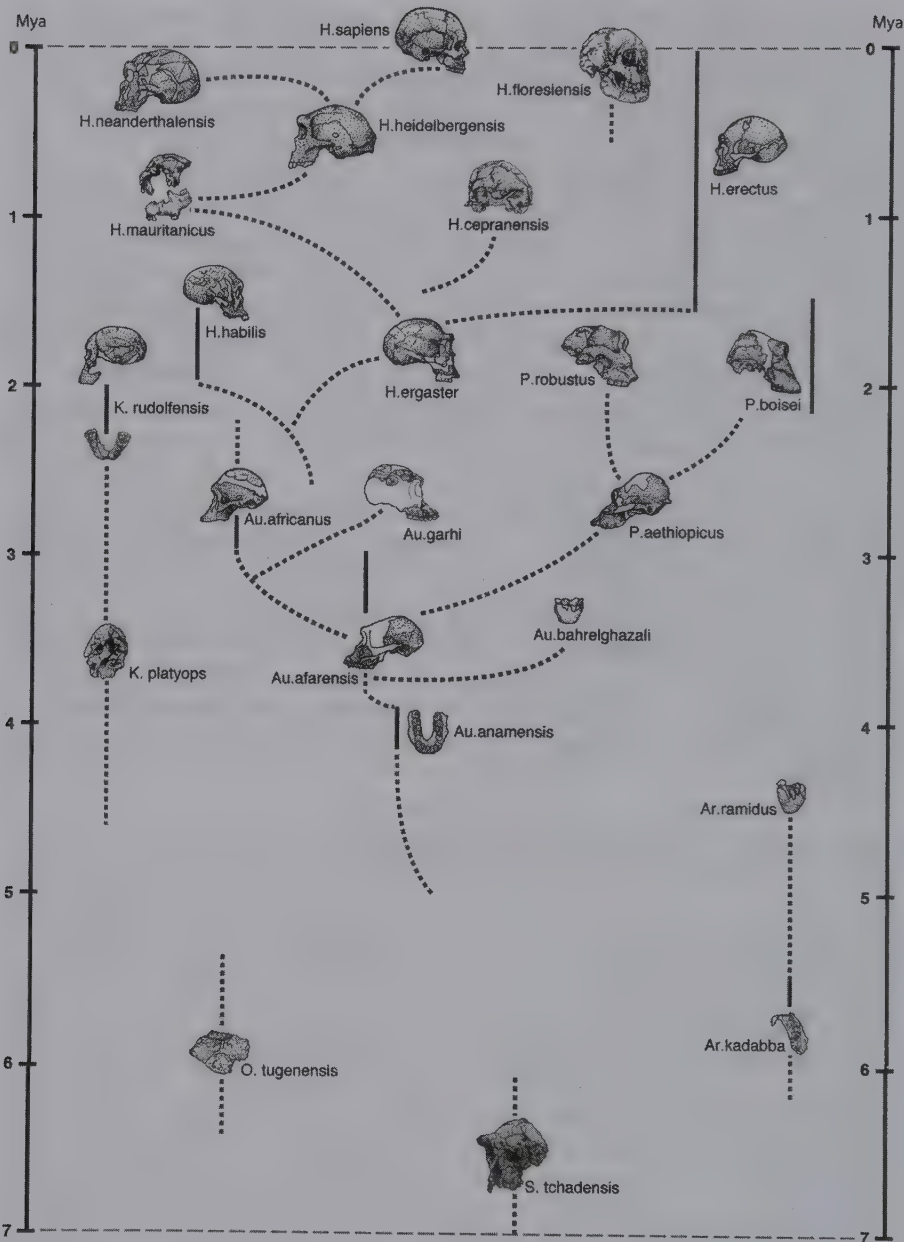
Still, one can start a chronological account of the human family with one uncontested taxonomic generalization: the very early hominids that have been reported since 1990 are a hugely diverse lot. There is no doubt that the four or five contenders in the 6- to 4-myr range—*Sahelanthropus tchadensis*, *Orrorin tugenensis*, *Ardipithecus ramidus/kadabba*, and *Australopithecus anamensis*—are all very distinctive creatures when compared both to each other and to hominids that came later. The major systematic question this motley assortment poses is not whether there were or were not multiple lineages of bipedal hominoids around shortly after the human lineage was born; it is whether or not all of these claimants to early hominid status were indeed hominids in the strict monophyletic sense. Lacking any clear idea of what we expect the stem hominid to look like, we are not currently in the best of positions to resolve this uncertainty.

Moving forward in time, there exists no recent minimalist appraisal of the number of australopith species. But I would guess that since the demise of the single-species hypothesis not many paleoanthropologists (if any at all) would recognize fewer than around five in addition to *Australopithecus anamensis*: *A. afarensis*, *A. africanus*, *A. garhi*, *P. robustus*, *P. boisei*, and *P. aethiopicus*. Other australopith species are out there for the more adventurous: *Australopithecus bahrelghazali*, *Paranthropus crassidens*, and *Praeanthropus africanus* among them. However many species there actually were, what is already clear is that the topography of relationships among the australopiths is too complex to be accommodated by the simple traditional "gracile/robust" dichotomy into which it's tempting to continue shoehorning the evidence. As far as we can tell these early, small-brained "bipedal apes" were all to one extent or another ecologically generalists, and their many species constituted variations on a single though pretty eurytopic theme. What we very tellingly do not see, though, is evidence among them for any notable trend over time towards significantly greater "modernity."

On top of these familiar cast members, in the general australopith time period it is now also necessary to add to the hominid roster the genus *Kenyanthropus*, with the two species *Kenyanthropus platyops* and *K. rudolfensis*—forms that nobody has any idea whether to describe as “australopiths” or not. Convenient as this informal latter appellation certainly seemed to be when Clark Howell started using it in the 1970s, it is now shaping up to be as much a hindrance as a help in understanding the diversity of the early hominid record. What it is safe to say is that *Kenyanthropus* adds significantly to known hominid diversity within the 4.0- to 1.8-myr period. But the nature of the connection (if any) between its two species, separated by the best part of 2 myr, and each epitomized by a cranium or crania in substantially less than ideal states of preservation, will doubtless be debated for a long time.

Within the genus *Homo*, by contrast, unrepentant minimalists still appear to accept a mere two species: *H. habilis* and *H. sapiens*. In essence, this would reduce the number of species lying between ourselves and the bipedal apes to only two. This is a ludicrously inadequate figure, given both the huge range of bony and dental morphology we see among the fossils attributed to *Homo*, and what is known about the degrees of difference that are typically found among closely related living mammals. In addition to the two species just cited, a more mainstream assessment of the genus *Homo* would nowadays also include the following: *Homo ergaster*, *H. antecessor*, *H. heidelbergensis*, and *H. neanderthalensis*, and perhaps also *H. cepranensis* and *H. floresiensis*. Braver souls might add *Homo georgicus*, and the bravest of all *Homo rhodesiensis* and *H. helmei*.

The plot thickens, though, when we examine the gray area that lies between the australopiths and *Homo*. This is not only because all fossils from the 2.5- to 2.0-myr period possess at best only tenuous morphological claims for membership in our genus, but also because, as Wood and Collard pointed out, there is no evident reason why it should include such forms as the gracile fossils from the lower levels of Olduvai. The Olduvai remains were initially allocated to our genus because of presumed stone tool manufacture, a fractional increase in brain size relative to *Australopithecus*, and, perhaps above all, because of Louis Leakey's desire to justify his longstanding belief in the ancientness of the genus *Homo*. In no other group of mammals would considerations of this kind have been accepted as justification for grouping species as unlike as *habilis* and *sapiens* together in the same genus; and even though the taxonomic game seems doomed forever to be played in Hominidae by its own distinctive set of rules, once paleoanthropologists have absorbed Wood and Collard's proposal to eliminate from *Homo* the species *habilis* and *rudolfensis*, the way will be open to develop a more rational view of what *Homo* is. Similarly, since the cause of rational taxonomy in Hominidae would hardly be served by tossing the the pair into *Australopithecus*, a reorganization of this kind should also logically spur a reevaluation of early hominid diversity at the genus level—and that again would be a most salutary thing.



Highly provisional evolutionary tree showing some possible lines of ancestry and descent among generally recognized hominid species. ©Ian Tattersall.

In the decades after Ernst Mayr told them to do so in 1950, paleoanthropologists dutifully strained to cram as many as possible of the hominids of the 2.0- to 0.5-myr period into *Homo erectus*. As the fossil record expanded, however, it became increasingly obvious to many that hominid morphological diversity during this period was too great to be accommodated within a single Old World-wide species of the genus *Homo*. The first significant acknowledgement of this came in 1975 when Groves and Mazak created the new species *Homo ergaster* to contain the 1.5-myr-old KNM-ER 992 jaw from East Turkana. Although this move was initially widely decried, the new name has by now been adopted by many to denote what had been known as "early African *Homo erectus*." A closer look, however, reveals something additional: not only are the various African fossils of this kind indeed quite distinct from the Javan type material of *Homo erectus*, but the African assemblage is, in itself, quite heterogeneous. For example, neither the dentition of the ER 992 type mandible of *Homo ergaster* nor the single preserved upper molar of the ER 3733 skull matches its counterpart in the WT 15000 "Turkana Boy" cranium. Further, there are significant morphological differences among the WT 15000, ER 3733, and 3883 crania, all of which suggest that the possibility of systematic diversity in this assemblage should at least be investigated.

There is also significant morphological heterogeneity in the classic Asian *Homo erectus* sample (Java plus Zhoukoudian and its like), although all clearly represent members of the same endemic Asian clade. The Dmanisi hominids from the Caucasus have also been allocated to *Homo erectus*, but all the crania so far described from Dmanisi show significant differences from the African material, and new finds and analyses will probably show that the allocation of the D 2600 mandible to the new species *Homo georgicus* was a wise move.

For a truly cosmopolitan hominid species we thus have to wait for *Homo heidelbergensis*, which, following its initial appearance at Bodo in Ethiopia some 600 kyr ago, spawned diverse variants in Africa (Kabwe, Saldanha), Europe (Arago, Petralona), and Asia (Dali, Jinniushan). This species may lie at or close to the origin of the European and African lineages that led to the Neanderthals and modern humans, respectively. In Europe, the earliest hominid fossil yet known is a fragment of the front of a mandible some 1.2 or maybe even 1.4 myr old found at the Sima del Elefante at Atapuerca in Spain. Its describers are so far noncommittal regarding its affinities, but it provides biological confirmation of the archaeologists' contention that hominids had penetrated western Europe by this early date. Prior to this find the earliest Spanish hominid had been the 780-kyr-old *Homo antecessor* from the Gran Dolina, also at Atapuerca, which in turn may well represent the same species as the *Homo mauritanicus* jaws from Tighenif in Algeria. The scientists who described *Homo antecessor* argued that this species lay at the root of both the Neanderthal and *Homo sapiens* lineages, but it is equally if not more likely that the Sima del Elefante and the Gran Dolina finds represent one or more early hominid incursions into Europe that ultimately failed to persist there. The same can probably be said for the

900-kyr-old Ceprano calvaria from Italy. This specimen has been allocated to the species *Homo cepranensis*, and it may compare most closely to the penecontemporaneous Daka calvaria from Ethiopia.

At one time it was thought that in Europe subsequent events were simple, the proto-Neanderthal group evolving in stately isolation. The expanding record now makes things appear otherwise. The earliest clearly identifiable Neanderthal relatives—hominids with some of the characteristics typifying the Neanderthals, but not all of them—are known from the Sima de los Huesos at Atapuerca. Recently redated from about 400 kyr to in excess of 500 kyr old, these hominids (which have been very misleadingly dubbed *Homo heidelbergensis*) actually lived contemporaneously with that morphologically distinct latter species, showing that at least two hominid lineages occupied Europe concurrently at that time. This may be a case of an ancestor persisting for some time (possibly quite a long time) beside its descendant; or, perhaps more likely, the ancestors of both European hominid lineages immigrated into the subcontinent following an earlier divergence in Africa or possibly in western Asia. Ultimately, the *Homo heidelbergensis* lineage seems to have petered out in Europe, while the Neanderthal clade flourished and diversified: the German Steinheim cranium, at least, seems to belong to the same group as, but nonetheless to be distinct from, both the Sima hominids and *Homo neanderthalensis*.

Given all this, the emerging picture seems to be that, once hominids had left Africa at some time between about 2.0 and 1.8 myr ago, they energetically diversified in the new regions they occupied. This is, of course, exactly what would be predicted for any successful mammalian group. The same would also be expected for the hominid populations that remained in the enormous African continent; and this, too, appears to be borne out by the evidence. Sampling is rather spotty; but there is a great heterogeneity of morphology among the increasing number of African hominids of the 1.0- to 200-kyr period, with entrants by now as diverse as Daka, Olgorgesailie, Ileret, Ndutu, Ngaloba, and Florisbad (*Homo helmei*), not to mention the classic Kabwe *Homo heidelbergensis* (or *Homo rhodesiensis* if you prefer: either way, the two forms belonged to the same very close-knit clade). Clearly in Africa a great deal was going on in the human evolutionary arena over this period, although in the absence of an adequate systematic framework it is hard to say just what this was. Whatever the exact geometry of events, however, it is out of this ferment that our own species, *Homo sapiens*, ultimately emerged.

The recent Sawyer/Maley reconstruction of an entire composite Neanderthal skeleton has drawn attention to just how derived our species *Homo sapiens* is in its bony structure, not just cranially but postcranially as well. And although comparative evidence is sparse, it seems that in body form, at least, *Homo sapiens* is uniquely derived. In theory, then, it should not be difficult to spot an early *Homo sapiens* in the fossil record. Alas, things turn out not to be that simple. A whole suite of bony characters distinguishes the skull of *Homo*

sapiens. Among these features, perhaps the most striking are our bipartite brow ridges (obliquely separated into medial and lateral components) and our chins—which are not just protuberances in the centerline of the jaw (you can find these elsewhere), but complex structures in the form of an inverted T. Oddly enough, though, in the late Pleistocene of Africa is known a number of skulls that meet all of the bony criteria of *Homo sapiens* except the bipartite brow ridge and the chin. These include the very earliest modern *Homo sapiens* yet claimed (Omo 1, recently redated to 195 kyr ago) and possibly the next-earliest, Herto (160 kyr)—although the latter lacks a lower jaw and it is not clear from available descriptions and illustrations whether the brow ridges are bipartite or not. Specimens that lie more firmly in this category (Boskop, Peers Cave, and Border Cave 5 among them) are younger, some of them probably very much younger. It is hard to know exactly what to make of this evidence; but whether or not more than one hominid species was involved, what may be said is that something anatomically very similar to *Homo sapiens* was around in Africa by almost 200 kyr ago, and that unequivocal anatomical *Homo sapiens* was in existence by about 100 kyr ago, the 93 kyr Levantine Qafzeh 9 being the best example.

Becoming Human

Even having established that the hominid evolutionary story is overall one of diversity rather than of linearity, we must still admit that an unbroken line of succession must have connected *Homo sapiens* to the very first hominid some 7 myr ago. What were the major events along the way, particularly events demonstrating advances toward the unique human cognitive condition that gives us such a powerful subjective sense of being *different* from the rest of the living world? Well, currently the *de facto* criterion for membership in the hominid family is terrestrial upright bipedal locomotion, and at the present state of play it seems cavalier to argue about this. Outside birds and their relatives, terrestrial bipedalism is rare indeed in the animal kingdom. What might it have been that caused an arboreal African hominoid to adopt upright locomotion on the ground under pressure from a changing habitat? Enormous amounts of ink have been expended in championing one aspect of behavior or another as *the* key to walking upright on the ground. If you are forced out of your ancestral forest habitat by its fragmentation and conversion to grassy woodland, standing and walking on two legs allows you to see predators from farther away, or to carry things with your hands, or to minimize heat absorption in the tropical sun, or maybe even to expend energy more efficiently, though this last advantage is highly debatable. Still, though like a meerkat you might want to stand upright occasionally to see further during those times you are on the ground, the only reason why you would commit yourself to walking around on two legs in the hazardous terrestrial environment is that you were *comfortable* doing it. If you weren't, at the first sign of trouble you'd

drop to all fours and scamper away. And the only reason a four-limbed creature would feel comfortable moving on the ground with its trunk held erect is that it already habitually did the same thing in the trees. Almost certainly, the hominoid whose descendants became the first hominids was an upright and probably thus suspensory arboreal forager.

Obligated by circumstances to spend increasing amounts of time on the ground, a habitually erect creature would have found *all* of the potential benefits of upright terrestrial bipedality—as well as all of its *disadvantages*—at its disposal. It is probably useless to debate which particular advantage was the key to the success of this terrestrial posture, although all of them need to be considered in developing any coherent notion of the lifeways of the earliest hominids. Still, it's worth noting that one big advantage of early hominid terrestrial bipedality that is often ignored in this context is that it helped preserve the ancestral ability to move around in the trees (interestingly, the less terrestrially committed great apes achieved an equivalent adaptability by evolving knuckle-walking *specializations* of the hand, something that the early hominids never had to do). And, as far as we can tell, the early hominids made the most of their dual arboreal/terrestrial facility: for as much as 5 myr the basic early hominid structure (and hence presumably lifestyle) seems to have persisted essentially unchanged—even as numerous species entered and left the evolutionary arena. Nonetheless, it is clearly terrestrial bipedality that was an essential precursor to everything in human evolution that was to come.

Cognitively, what was going on in this early period is hard to know. To say that we have no evidence that the early “bipedal apes” (with their short statures, large faces, small brains, and archaic body proportions) had surpassed the cognitive level typical of today's apes is not to be dismissive. With almost every day that passes comes news of some other great ape propensity that we had previously imagined unique to ourselves: tool manufacture, forward planning, and use of spears and digging implements. Cognitively speaking, today's great apes are very considerable beings; if by analogy from brain:body size ratios we can view their mental capacities as approximations for those of the early hominids, it means that our earliest forerunners were almost certainly more complex beings than any others on the planet in their time. Still, it is not for several million years, not until the inauguration of the archaeological record with the invention some 2.6 myr ago of stone tool making, that we can be sure that early hominids had achieved a cognitive level beyond that of any nonhuman primate on Earth today. Despite their remarkable capacities, and even with intensive training, no apes have yet quite mastered the understanding of the mechanical properties of stone and of cause-effect relationships that is evident in the spontaneous invention of stone tool making by an early hominid—perhaps the greatest inventor ever. What's more, the degree of foresight shown by early stone tool makers, who carried lumps of stone around with them for long distances in anticipation of needing them for tool manufacture, is not yet matched by anything observed in apes. Yet the early

tool makers were almost certainly large-toothed, small-bodied, small-brained, and of archaic bodily proportions. And if this is so, we see here, at the very beginning, evidence of a pattern that has characterized hominid evolution ever since: that biological and technological innovations are typically decoupled in time. No matter how convenient or intellectually neat it might be to do so, there is no instance in which we can “explain” the introduction of any new technology by the arrival of a new hominid species—and this actually makes eminent sense; for behavioral innovations clearly have to be made within pre-existing species.

Nonetheless, while from the cognitive and technological viewpoints the invention of stoneworking looks like a truly momentous innovation, at the time it may simply have enabled hominids to do what they had always done, if maybe a little bit better. As, indeed, new generations of technology have continued to do ever since, each one building on the one that preceded it—and each tending also to persist alongside its successor. Apparently, the ways in which technological innovations affect lifestyles may be quite subtle, and it is perhaps in this context that we can best understand how it was that small-brained, primitive-bodied early hominids began to make stone tools, yet continued to look (and presumably live) pretty much as they had for millions of years. Perhaps yet more remarkably, it's not even clear that the arrival of modern body proportions heralded any major lifestyle changes among hominids; for the first *Homo ergaster* continued to make tools that were more or less indistinguishable from those of the archaic bipeds, and there is not much evidence for other behavioral developments, either. This isn't to deny that, uprightness apart, the arrival of *Homo ergaster* marked the single most important transformation below the neck in the entire course of human evolution. Clearly it did, and the change also apparently happened fast: something that it is easier to comprehend now that we know that small changes on the structural genetic or transcriptional levels can have major cascading effects throughout the developmental process. And while the archaeological traces are largely mute on the matter, the consequences of the acquisition of the new body form are evident in the fact that, hard on its heels, hominids had contrived to spread for the first time far beyond the bounds of their natal continent. The 1.8-myr-old hominids of Dmanisi (with their smallish brains and very crude stoneworking technology) were of much shorter stature than the Turkana Boy, but nonetheless are reported to have shown modern features in their postcranial skeletons. Evidently, emancipated by the new striding body form from the woodlands and forest edges to which they had apparently been confined earlier, hominids were at this early time able to traverse ecological zones that had earlier served as barriers to movement.

Homo ergaster, or forms like it, had been around for several hundred thousand years before any archaeological evidence shows up that they were using their enlarged brains in any significantly new way. This evidence takes the form of the appearance, at around 1.5 myr ago, of Acheulean stone tools, the first

implements to have been made to a “mental template” that existed in the mind of their makers. Oldowan toolmakers—as many Acheuleans also continued to do—had, in contrast, been most interested in producing sharp stone flakes that they could use as cutters and scrapers. They were thoroughly aware of the principles of striking stone at the correct angle for producing such flakes, but they were not concerned to produce tools of particular shapes. The Acheuleans were, however—and they came to revel in it. Identical handaxes litter many African localities in almost unimaginable abundance, and at sites such as Tanzania’s Isimila they may be of extraordinary size—in some cases too heavy to lift with one hand. Apart from showing us that the toolmakers were pretty strong—for the shaping of large stone cores of this kind demands prodigious power—such tools as those from Isimila maybe even show a sense of humor, or at least a sense of pure design: some of these tools were simply too large to use, certainly with any deftness. Such caprices apart, however, the Acheulean handaxe has been aptly described as the “Swiss Army Knife of the Paleolithic,” serving a diversity of functions such as cutting, hacking, scraping, and digging. And its manufacture endured for well over a million years.

There’s little doubt that with the invention of bifacially flaked tools such as handaxes we are witnessing yet another major cognitive leap on the part of mankind. But, once again, this development was apparently independent of any other major innovation—biological or even cultural. For example, even once the Acheulean was well established, most archaeologists are reluctant to conclude that *Homo ergaster* or its later relatives ever systematically hunted large animals. The stone tools themselves apart, the leavings of Acheulean hominids didn’t differ a lot from those of their predecessors, though the way they are distributed across the landscape perhaps suggests wider ranging. Once again, then, we find the persistence of a general lifeway even in the presence of technological refinements that one might have expected to do more than merely permit it to be carried out more efficiently, and maybe safely. It’s fair to remark, however, that the advent of such cognitive innovations as “mental templates” might well have changed the rules of the natural selection game by putting a premium on abstract intellectual skills and might thus have deeply influenced future biological and cultural developments.

This may in fact be one key to the obvious question that much of the preceding discussion raises: if general lifeways changed so little prior to the advent of *Homo sapiens*, why do we see such a marked tendency to brain enlargement among hominids over the past 2 myr or so? One possibility is that even relatively small technological advances—changes simply in the way in which the manipulability of the world was viewed by hominids—may have handed an evolutionary advantage to those individuals capable of grasping and exploiting them. This would quickly have affected the composition of the small groups and populations in which early humans lived, and in their turn the rapidly fluctuating climates—and geographies—of the Pleistocene would

have promoted a rapid process of sorting among those populations. The question is complicated, however, by the fact that we see brain enlargement happening apparently independently in several different hominid lineages over this time. Successive populations of *Homo erectus* showed consistently enlarging brain sizes in their isolated southeastern Asian enclave; members of the Neanderthal clade in Europe apparently showed brain size expansion with time, and, even though details are sparse, it is evident that the African lineage leading to *Homo sapiens* displayed a similar phenomenon.

Brain tissue is metabolically expensive, so there must have been some very considerable advantage to larger brains. Presumably the dividend was received in terms of greater "intelligence," although precisely what this might have meant in terms of abilities or context remains unclear. What is even less clear is whether brain size increase reflected some kind of within-species dynamics, possibly mediated by social factors as has been widely speculated, or whether it was the outcome of the preferential survival of larger-brained hominid species or populations. Deciding between these alternatives is difficult at present, but perhaps the larger-scale latter process is somewhat more probable in light of the repetition of this remarkable phenomenon across a wide taxonomic range. It will also be important to understand why *Homo floresiensis*, if a real taxon, bucked this trend. Whatever the mechanism involved, however, comprehending it is absolutely key to knowing why such a sharp upturn occurred in the overall hominid brain:body size curve following about 1.8 myr ago. And a necessary prerequisite to this will be a keener understanding of hominid systematics in this period.

Following the invention, about 1.5 myr ago, of handaxes and related bifacial implements such as picks and cleavers, we have to wait another half-million years before we encounter any notable advance in stoneworking technology. And even here, change expressed itself simply as a refinement of the basic handaxe-making technique. At about 1.0 myr ago, handaxes began to be made thinner, using a technique known as "platform preparation," in which the axe's edge was initially made less oblique to provide a surface at which more force could be directed. This advance was associated with at least occasional use of "soft hammers," made of soft organic materials—bone, wood, antler—rather than of brittle stone. Who was responsible for this invention? We don't know, for associated hominid fossils don't exist. But we can be pretty sure that these early hominids had considerable powers of intuitive reasoning because, as Kathy Schick and Nick Toth point out, platform preparation is not an intuitively obvious procedure. Which raises a question we've so far avoided: Could these advanced Acheuleans be described as human? In a strictly legalistic sense, I suppose they must be considered *ex officio* humans, as members of the genus *Homo*. But that's not to say that we would intuitively recognize them as such if we were to encounter a group of them while out for a stroll on the savanna. In the absence of an agreed functional definition to tell us what is

human and what is not, everyone has to make up his or her own mind; what is certain, however, is that even the latest Acheuleans were very far from *fully* human as we are today.

Approaching the end of the Acheulean's heyday brings us to the period in which hominid brain sizes were inching up close to the modern average, which is the principal reason why most hominid fossils of the last half-million years or so used to be described as "archaic" forms of *Homo sapiens*. Yet hominids of this period looked very different from us from the neck up, with foreheads retreating behind large undivided brow ridges and large faces with biggish teeth (compared to *Homo sapiens*) that were hafted in front of the braincase rather than beneath it. We have no good associated skeletons to tell us exactly what these hominids were like below the neck, but a composite snapshot from Atapuerca's Sima de los Huesos suggests very substantial robusticity.

With *Homo heidelbergensis*, represented by fossils from sites as far apart as Kabwe in Zambia, Bodo in Ethiopia, Arago in France, Petralona in Greece, and Dali and Jinniushan in China, we encounter what is probably the Old World's first cosmopolitan hominid species. Dating of most of these specimens is imprecise, but in the same general time range of 600–200 kyr ago we also find (in addition to late-surviving *H. erectus* in Java) fossils such as those from Nduetu and Atapuerca, whose morphology does not fit comfortably within *H. heidelbergensis*. Again, the picture is one of diversity: clearly, the lonely status of *Homo sapiens* as the world's only hominid is highly atypical and may well be telling us something very fundamental—and possibly quite alarming—about ourselves and our uniqueness.

Some of these new kinds of humans (especially outside Africa) are associated with remarkably rudimentary stoneworking technologies, but in the 200- to 300-kyr time range we begin to encounter a much more sophisticated way of working stone involving "prepared cores." In this technique a lump of stone was fashioned in such a way that a single final blow (usually with a soft hammer) would detach a "flake" that represented a quasi-finished tool. This was a considerable advance, for it ensured the production of a long, continuous cutting edge around almost the entire periphery of the tool. The regular domestication of fire in hearths began a bit earlier (790 kyr in Israel is the earliest date, but the practice only became commonplace following about 400 kyr ago); at the latter date we also begin to pick up evidence for domestic structures such as huts. From the same time come those wooden spears from Schoeningen, which may imply an earlier arrival than formerly assumed of sophisticated ambush-hunting techniques. Earlier yet, we are presented with apparent evidence for cannibalism at the 780-kyr-old Gran Dolina of Atapuerca; and intentional defleshing is reflected in stone tool cut marks on the forehead and within the orbit of the *Homo heidelbergensis* cranium from Bodo. Clearly something was moving on the cognitive front during the middle Pleistocene, however dimly we perceive it; but it is important to stress that

throughout this period we see nothing that is uncontestably a symbolic object. From this point on, too, stone tools began to decrease in size, although some of the older forms were preserved; for example, small handaxes were made on flakes, rather than on large cores broken off much larger boulders as was the practice in Acheulean times. Other flake tools might have been hafted onto handles or spear ends.

The apogee of prepared-core tool making was achieved by the Neanderthals, whose beautifully crafted Mousterian tools came in a large variety of forms. *Homo neanderthalensis* is not a particularly close relative of *Homo sapiens*—it looks right now as if the last common ancestor of the two species lived well over half a million years ago—but for three reasons the Neanderthals are critical in helping us understand just what it is about *Homo sapiens* that makes it so unusual. First, they independently acquired brains that were as large as our own (indeed, at 1740 ml the Amud Neanderthal skull from Israel has the largest cranial capacity ever measured in a hominid fossil, though it can be matched in living *Homo sapiens*). Second, they left behind a much fuller archaeological record than we have for any other hominid species barring *Homo sapiens*. Third, they shared their territory with *Homo sapiens*, at least for a time. For all these reasons the Neanderthals offer us the best yardstick we have by which to judge our own uniqueness.

Cognitively, the Neanderthals were clearly complex beings. They constructed shelters and manufactured compound tools. They used ochre (though in what context is unclear) and clearly had an aesthetic sense, picking up fossils, for instance, or carrying attractive but useless pieces of stone for long distances. They undoubtedly had clothing and other technologically sophisticated ways of dealing with the often harsh environments in which they lived. At least occasionally, they buried their dead (if simply), and looked after the disadvantaged. The isotopic evidence suggests that at least at some times and places they were highly specialized carnivores, even specializing in the hunting of such massive and intimidating beasts as woolly rhino and mammoth. There is, in other words, much to admire about the Neanderthals. But one thing that is strikingly absent from the record of their lives they left behind is evidence of symbolism (except, perhaps, in the Châtelperronian and comparable “postcontact” cultures, where the evidence is both limited and arguable). It takes a certain amount of special pleading and extended inference to conclude that the Neanderthals were symbolic creatures. Indeed, it is highly likely that those who, in light of their large brains, wish to view these hominids as an unusual version of ourselves, are actually doing them a disservice by robbing them of their own unique identity. Rather than welcoming them into the human fold as by implication an inferior version of ourselves, perhaps we would do them greater justice by viewing them as the most advanced expression ever achieved among hominids of what an intuitive, nonsymbolic, nondeclarative intelligence can do. For the record clearly shows that cognition of Neanderthal kind can take you a very long way.

The Cro-Magnons who entered Europe following about 40 kyr ago, and who apparently displaced the Neanderthals in the process (exactly as their kin were doing concurrently and a bit later in eastern Asia to *Homo erectus* and the Flores hominids, respectively), came into the subcontinent with all of their symbolic capacities in place—and soon they flaunted those capacities as brazenly as any society since. The contrast in late Pleistocene Europe between the two large-brained species *Homo sapiens* and *H. neanderthalensis* thus dramatizes the cognitive gulf that separates us from our closest living relatives today. The gap has dramatically narrowed compared to earlier hominids, it is true, but the essential difference is still there.

Remarkably, this is also true for the first *Homo sapiens* that we find in the fossil record: the Omo and Herto finds are associated with unimpressive stone tools, and there are no unequivocal hints of symbolic behaviors among hominids anywhere at that early time. The same may be said of the later early *Homo sapiens* from the Levant: at 93 kyr the Jebel Qafzeh 9 burial is associated with a stone tool kit identical to the kit Neanderthals had been making in the region for many thousands of years and would continue to make there for tens of thousands of years more. Indeed, the first stirrings of symbolism (such as the engraved plaque from South Africa's Blombos Cave) are seen in the archaeological record notably later than the establishment of *Homo sapiens* as a distinctive physical entity. There was a clear sequence involved here: first, the appearance of anatomically recognizable *Homo sapiens*; then, after an extended interval, the emergence of the symbolic being we know today.

Richard Klein has eloquently argued that this apparent decoupling of biological from cognitive innovation was due to a late-occurring genetic change that affected our precursors' neural circuitry but was unreflected in their osteology. However, as we have seen on numerous occasions throughout this book, such decoupling has been a routine matter throughout hominid evolution, based on the phenomenon of exaptation—the plain fact that any novelty has to come into physical existence *before* it can be recruited to a new function. In the case of *Homo sapiens* it seems most parsimonious to conclude that, in the wide-ranging genetic/developmental reorganization that saw the appearance of *Homo sapiens* as a physically distinctive entity, there was also involved a neural change that created the potential for symbolic thought. Intellectual business continued as usual, however, until some cultural stimulus intervened to initiate symbolic processes in the human mind. Just what this cultural stimulus might have been must remain speculative; but the strongest candidate is the invention of language—which is, after all, the ultimate symbolic activity, involving as it does the formation and recombination of mental symbols according to a set of rules. Modern symbolic thought is almost inconceivable in the absence of language, and vice versa. Language, we know, can be spontaneously generated; and as an externalized communal property it is a better candidate for a cultural stimulus that ultimately affected an entire

species than are other leading contestants for this role, including theory of mind which is internalized.

Whatever the case, though, it is clear that modern symbolic thought, which is of both recent and apparently short-term origin, is not simply an extrapolation of any evolutionary trend that preceded it. Clearly, its acquisition built on an enormously long evolutionary history dating back to very origin of vertebrates. It would not have been possible in the absence of all the very many events in that history; but it was not *predicted* by any aspect of that history. Its appearance can only be explained by emergence, whereby a new level of complexity, something entirely new and unexpected, comes about from a chance combination of features. Like a keystone in an arch, a relatively small (we suppose) neural modification or addition gave rise to a structure with an entirely new potential. The acquisition of symbolic cognition was not, in other words, the ultimate outcome of a linear process of long-term refinement.

Reviewing the Paleolithic archaeological record, then, it is hard not to conclude that there was, at least cognitively speaking, but one great leap forward in human evolution: the one that gave rise to the recent, symbolic, version of our species *Homo sapiens*. If you'd been around at most earlier stages of human evolution, with some knowledge of the past you might have been able to predict with reasonable accuracy what was coming up next. Behaviorally modern *Homo sapiens*, however, is emphatically not an organism that does what its predecessors did, only a little better. It is something very—and potentially very dangerously—different. Something extraordinary, if totally fortuitous, happened with the birth of our species. And although the human biological past stretches back over six myr or more, it is the exact nature of that very recent yet still obscure happening that poses the true enigma of human evolution.

Epilogue

I have just said that in the case of the species *Homo sapiens*, perhaps for the first time, past performance has been no guarantee—or, at least, no predictor—of future results. But can we hazard anything about our future as a species from looking at the general rules that govern the evolutionary process—for, extraordinary as we are, there's no reason to believe that we have become emancipated from them. Despite a limitless amount of historical evidence to the contrary, human beings appear to have enormous difficulty in ridding themselves of the notion of their own potential perfectibility. One way in which the perfection of mankind might be realized is particularly beloved of science fiction writers, who regularly proffer visions of future people with huge brains whose rational qualities actually manage successfully to assert themselves over more atavistic, emotional, instincts. But is it in fact at all reasonable to contemplate a future in which evolution will, as it were, ride in on a white horse to rescue us from ourselves? A moment's thought shows how unlikely this is. Everything that we know (as opposed to assume) about the evolutionary process indicates that population fragmentation (followed by genetic innovation and speciation) is a prerequisite for the accumulation of any significant evolutionary change in mammals. Yet we are living at a time when the human population is becoming denser by leaps and bounds, and when individual mobility has become incomparably greater than ever before. *Homo sapiens* today is in a mode of intermixing rather than of differentiation; and the conditions for significant evolutionary change simply don't exist (and won't, short of some all-too-imaginable calamity). In the demonstrable absence of perfectibility, if that calamity is not to occur we shall have to learn to live with ourselves as we are. Fast.

Lest this prospect be thought unbearably dismal, however, it is worth reminding ourselves that the history of mankind over the past hundred thousand years has essentially involved the replacement of a process of sporadic biological innovation by a rather different progression of continuous cultural and technological change. Instead of waiting patiently for the next biological novelty to come along, we have been ceaselessly exploring how to exploit the apparently inexhaustible symbolic capacity we already have. And inexhaustible it certainly seems to be: the fun is far from over.

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At some level the contents of this book reflect everything I have read in paleoanthropology over a long career. The following list identifies most of the major books and articles referred to in the text, including all those from which direct quotations have been taken. Works bearing asterisks are easily accessible reviews and/or contain extensive bibliographies. For convenience, references from each chapter of this book are listed together.

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